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THE FOUNDER OF AMERICAN PARASITOLOGY, JOSEPH LEIDY

Most fields of biology are opened up gradually, at least to the extent that pioneer workers patiently accumulate data, usually in the form of disassociated and unrelated observations and isolated details, before the time is ripe for the master mind which builds of this inchoate material a new part of the great structure of science. The field of parasitology in America constitutes a striking exception to this general principle. Prior to 1846 no one in this country appears to have devoted any attention to the subject and the few casual notes on parasites which have been dug out of earlier writings on other topics are too scanty and superficial to furnish foundation material for any study. Accordingly when in that year a young Philadelphia physician, scarce 23 years of age, began to devote his attention to studies on parasitic worms, he found himself confronted with the double task of gathering the material and of organizing it into scientific form. Moreover, while in some other fields in which he published other investigators added interest and zest by their contributions, here he worked alone and it was more than a quarter of a century before any other student in this country contributed in other than casual fashion to the subject of parasitology. Yet the work he undertook was performed so thoroughly that the descriptions and interpretations he published within the decade from 1846 to 1856, sufficed not only to lay the foundations of American parasitology, but also yielded him recognition as an authority in that field everywhere and contributed materially to the advancement of the subject in Europe where it had been studied intensively for more than half a century.

Joseph Leidy was born in Philadelphia on Sept. 9, 1823. Nature had endowed him admirably for the part he was to play. Sprung from a lineage that represented the best in two great nations of the old world, he inherited artistic skill of no common order, love of nature and life, keeness of perception, accuracy of judgment and that foresight truly characteristic of a master mind, which enabled him to predict successfully the decisions of the future. These conditions will stand out more clearly after a review of the general history of the family and the special training of the man.

THE LEIDY FAMILY

Following close after the pilgrimage of William Penn into the Rhenish Palatinate came to this country a wave of migrants from Germany that began about 1688 and contributed an important early element to the American stock. Among those who came were the first American ancestors of Joseph Leidy. In the old world the name was spelled variously, Leydig, Lydig and Leidig, and was anglicized later by the English authorities in Pennsylvania into Leidy.

As early as 1338 one of this name, Johan Leydig, was living at Wilsnach in Swabia. Among his descendants was a chief burgher of Wilsnach, Joachim Leydig, whose son, the Rev. Matthew Leydig, studied theology with Luther at Wittenberg and was ordained by him in 1550. In 1552 he was called to the German Reformed Church at Halle where he died in 1601. He published a translation of the Bible (Berlin, 1586) and later the Lutheran vespers and psalms of David. Another of the family, Joachim Leydig, also a native of Halle, served as pastor of the Reformed Church at Königsberg in Prussia, until in 1571 as the result of a doctrinal controversy he returned to Halle. Jacob Leydig, grandson of the Rev. Johan Leydig, and a scholar of note, published in 1677 a history of the ancient electors of Prussia. It was in this, the XVII Century, that armorial bearings were granted to the head of the house, Joachim Leydig, in recognition of his public services in founding a hospital. It is interesting to note that this same family has produced in recent years one other highly distinguished biologist, Professor Franz Leydig of Würzburg and Bonn whose great grandfather was a brother of Joseph Leidy's great grandfather.

Following the Thirty Years' War, the Palatinate was subjected to religious persecutions and as a direct result of these John Jacob Leydig emigrated from Wittenberg. He arrived in Philadelphia in 1729 and settled on a tract of 400 acres purchased from the Penns. This early settler, great grandfather of the naturalist, established a settlement known even to the present day as Leidytown, although the postoffice bearing this name is all that remains of the original town. His son, John Jacob Leidy, who fell heir to the homestead, found upon his land deposits valuable in the manufacture of pottery and utilized them so successfully that specimens of his workmanship of evident artistic merit are preserved in the exhibit of pottery of Colonial times at Memorial Hall, Philadelphia. During the American Revolution he served as an officer in the Pennsylvania forces and played an active part in the events of the war in that region. His wife, Joseph Leidy's paternal grandmother, was Marie LeFebre, a sister of Francis Joseph LeFebre a marshal of Napoleon I and a peer of France. To this joint French-German ancestry the grandson clearly owed many of the traits which enabled him to win such a conspicuous success.

His son, Philip Leidy, inherited his father's land, and at the close of the Revolution settled in the city of Philadelphia where he engaged in industrial pursuits with marked financial success. During the war of 1812 he served as an officer. After Marshal LeFebre's death, being deeply involved in military affairs, he named his sons Francis and Joseph, and hoped they would both seek fame in military careers. While the one son, Joseph, with whom this article is directly concerned, served with distinction in the Civil War, it was as surgeon in a military hospital and not in a position such as his father evidently had in mind.

Joseph Leidy's mother was Catherine Mellick (Moelich) who also was descended from natives of the Rhineland that had come originally to New Jersey and had later moved to Pennsylvania. She died when Joseph, who was her third child, was only twenty months old and he was reared by a stepmother, Christiana Mellick, of whose careful training Leidy often made grateful acknowledgement: "The only mother I have known," he said at one time, "she was all in all to me, the one to whom I owe all that I am."

THE STORY OF LEIDY'S LIFE

During his early education the boy manifested little ability in the classical studies which were standard in that day but showed an eager interest in natural history even though it was not included in the curriculum. In his wanderings into the country in search of minerals, flowers and insects he absented himself at times from school and was indifferent to those sports which tempted most boys. His leisure seems to have been devoted to drawing objects of natural history and a note book still extant and dated 1833 shows that even at the age of ten he had cultivated, alone by himself, that accuracy in observation and fidelity in delineation which gave its high value to his later work. His father was so deeply impressed by this phase of his work that he resolved to make an artist of the boy. His mother, who was a woman of marked intelligence and foresight, had a firm conviction that her sons should receive a professional education and as Leidy later stated, her strength "carried the point." His skill in making minute dissections already displayed on various occasions and his mother's confidence that she saw in him the traits which would make a great physician, led first to the study of anatomy under a private teacher and later to his matriculation at the University of Pennsylvania, where he received the degree of doctor of medicine in 1844. But professional duties proved irksome and were entirely abandoned two years later in favor of scientific pursuits.

The story of Leidy's active life and his relations to the Philadelphia Academy of Natural Sciences, with which his name is inseparably connected and to whose upbuilding and reputation he made most note-

worthy contributions in every department, has been so fully portrayed by contemporary biographers that the subject may be passed over here with a brief reference to the sources of information. Many biographical sketches of Leidy have been published. Among those of general scope that of Chapman (1891) which was read before the Philadelphia Academy soon after Leidy's death is rich in personal material and broad in its treatment of the career of the great naturalist. Some later sketches are marred by the introduction of unverified personal episodes. The most recent biography, prepared by H. F. Osborn for the National Academy of Sciences, paints a vivid and most satisfactory picture of Leidy "as the founder of vertebrate paleontology in America and as the last great naturalist of the old type." Osborn lists a dozen other biographical sketches, most of which handle Leidy's career from the viewpoint of a worker in some particular field without attempting to cover critically all the activities of this many sided man. Only one of these sketches, and that a brief one (Ward, 1900), essays to treat particularly Leidy's contributions in the field of parasitology. In 1917 Pfender published a valuable paper on the important contributions to medicine made by Leidy."[1]

An examination of the studies which have been made on Leidy's life and work justifies the criticism that in the main adequate consideration has not been given to the leading part he played in laying foundations and developing the field of parasitology, helminthology and medical zoology. This may be due in part to a failure of his biographers to recognize this as a distinct field of work and yet even this factor is not sufficient to explain the absence of appropriate emphasis on his extensive and valuable contributions to knowledge in this field. His earliest biographer, Chapman, who wrote very fully of Leidy's other work, offers little comment on the contributions made to parasitology. A short discussion of the work on Trichina and a single paragraph on the investigations on Gregarine structure, or less than a page in all, is devoted to recording studies of fundamental importance. And H. F. Osborn, whose biographic sketch of Leidy merits high praise, speaks of his "two chief lines of investigation, the Protozoa and fossil vertebrates." To be sure Osborn discusses under the heading of contributions to microscopy the studies in helminthology which deservedly brought to Leidy a world-wide reputation and later quotes from those studies and from the views of recent investigators to demonstrate the value of Leidy's work in parasitology.

But even with that the record does scant justice to Leidy's pioneer work in this field. The reason may perhaps lie in the fact that the

1. It is to be regretted that the admirable sketch by Dr. F. H. Garrison, of which I have just seen a copy, is printed where it must remain generally inaccessible.

development of the subject in America has even yet hardly reached the stage where a just estimate of Leidy's contributions to it can fairly be made. One writer quoted by Osborn speaks half apologetically of Leidy's work "from the point of view of a specialist of 1910." I cannot feel that such an attitude is justifiable and find much to indicate that Leidy was so far in advance of his generation in the field of parasitology, that only within recent years have students in this field come to the point of understanding his descriptions and beginning to see for themselves the things he described a generation back. No doubt these descriptions are often unfortunately brief and require restatement on the basis of repeated study to bring them fully into line with present day practices but they have in general come out well from such critical examination and the work gains in strength with such restudy. Abroad his work in this field was highly acclaimed both on the continent and in England. In an address in 1891 the president of the Linnaean Society of London refers to him as the most distinguished biologist of his time in America and adds that he contributed researches in helminthology and parasitology "of epoch-making importance." An extended biography of Leidy is in the course of preparation by his nephew, Dr. Joseph Leidy II of Philadelphia, and to him the author of this sketch is deeply indebted for data and suggestions as well as for a general revision of this manuscript to insure its correctness.

LEIDY'S PERSONALITY AND INTELLECTUAL POWER

All of Leidy's associates unite in ascribing to him a personality of a most engaging type so that when on April 30, 1891, he passed away at the close of a long and active life, he left not a single enemy but a multiude of friends. His interest and devotion to his scientific pursuits was marked by all and his enthusiasm as well as his power in presenting his observations, made him a welcome speaker at scientific gatherings and a most successful teacher in his college work. For many years he visited the public market on Wednesday and Saturday at 6 a. m. or earlier to inspect whatever was brought in and to examine specimens for parasites. The story of his finds was told so vividly as to impart interest to the most trivial item. Leidy's quiet humor, which crops out more than once even in his exceedingly brief articles and which is commented on by his contemporaries, is beautifully illustrated by the few lines which Minot quotes from Leidy's story of his field trips.

"'Going fishing?' How often the question has been asked by acquaintances, as they have met me, with rod and basket, on an excursion after materials for microscopic study. 'Yes!' has been the invariable answer, for it saved much detention and explanation; and now, behold! I offer them the results of that fishing. No fish for the stomach, but, as the old French microscopist Joblet observed, 'some of the most remarkable fishes that have ever been seen'; and food-fishes for the intellect."

The "fishes" that he sought were Rhizopods which formed the basis of the magnificent monograph well known to all workers in natural history.

In his love of facts and his desire to go more deeply into life after them, he was devoted to the microscope and used it with a sharpness of vision and keenness of critical interpretation that yielded splendid results in fields that in his day had not even been outlined, much less developed. In this connection consider his observations on regeneration in Planaria, on the foundation of the cell wall after division of the cell, or the intimate structure of the cell in Rhizopoda, on parasites of many sorts, on protozoa and protophyta in his Flora and Fauna, and consider that it was only 1849 when he published his discovery of the existence of bacteria in the intestine.

The number, variety and range of Leidy's discoveries gave him unusual opportunity for speculation which was, moreover, the order of the day. His views on such undertakings are succinctly expressed in the preface to a monograph on the extinct mammals of Dakota. Though the subject lent itself admirably to the exercise of scientific imagination, he held himself rigidly to a recital of the facts and stated frankly, "No attempt has been made at generalizations or theories which might attract the momentary attention or admiration of the scientific community." And yet with all that no critic would be justified in charging Leidy with lack of scientific insight or with limited powers for interpreting the discoveries he made. The apparently trivial item became significant in his eyes and in connection with many discoveries he pointed out this import in a definite way that sometimes waited years for confirmation and utilization. As conspicuous instances of this, his indication of the role of flies in spreading disease, the interpretation of the relation between the trichina in pork and human parasitism and the significance of the hookworm in the production of anemia, all furnish evidence, more fully presented elsewhere in this sketch, of the power to anticipate to a remarkable degree the development of scientific thought in entirely new and most significant directions.

Leidy was preeminently a student of structure and in its minute determination he shows himself a master. His thesis for the M.D. degree was on *The Comparative Anatomy of the Eye of Vertebrated Animals.* His fame as a paleontologist rests on the painstaking and thorough analysis of anatomical detail. It was this same characteristic which made his work on parasitology so valuable and so permanent even though his descriptions of the parasites were unfortunately meager and not accompanied by those unsurpassed drawings which make the North American Rhizopods at once a marvel and a sure support for the student.

Leidy's critical powers manifested themselves in the ability to recognize a group of structural features in a newly-encountered organism as distinct from a previously known combination of structures and to assign them an independent rank. In his day it was the custom to lump forms, to include a wide range of animals in a single genus for instance. Today it seems to be the fashion to make new genera on the slightest provocation. Now every worker follows naturally the practices of his age and it is not difficult to travel either road; but it requires genius to conform to the period in such fashion as to depart from its habits successfully when a later and better informed generation comes to pass judgment on the work. And that is precisely what Leidy did in parasitology. When European workers were crowding animals forcibly into vaguely defined genera, he working alone but with a keen eye for structural detail, saw that certain of the types he found could not possibly be forced into the time honored and universally accepted genera of his foreign confrères, so he made for them new genera and when Europe did not accept his findings he refused to rush into controversy but waited for time to decide. This work he did not in one group but in a wide range of forms and among the new genera he recognized and established one may cite the following as representative of his work in various groups:

Endamoeba, Dinamoeba, Ouramoeba, Nyctotherus and Trichonympha among the Protozoa; Phagocata, Catesthia, Anortha and Rhynchoscolex among the Turbellaria; Clinostomum and Cotylaspis among the Trematoda; Emea in Nemertines; Nema and Pontonema among the Anguillulidae; Streptostoma, Thelastoma, Hystrignathus and Synplecta among parasitic nematodes; Pectinatella and Urnatella in the Bryozoa, etc.

A few of these have suffered shipwreck on the rocks and shoals of nomenclatorial rules, but all were fundamentally sound and bear testimony today to the clarity of his conceptions of comparative anatomy.

Many striking instances could be cited to show how marvellously exact was Leidy's eye in detecting minute details of structure that escaped even the trained vision of other investigators. At the same time he manifested almost equally great powers in interpreting these observations. He was the first to include the Gregarines among animals and to describe certain minute fibrillae in those cells which he interpreted as the first traces of muscular structures. The older Van Beneden vigorously denied the existence of any such structures and it remained for his son many years later to confirm Leidy's observation and to acknowledge gracefully the father's error. In 1848 Leidy published a study on the comparative structure of the liver in which he advanced views at variance with the then accepted beliefs. His views were vigorously combated but have since been confirmed by embryological researches and are now generally accepted. In 1846 he found an encysted worm in the hog. He "could perceive no distinction

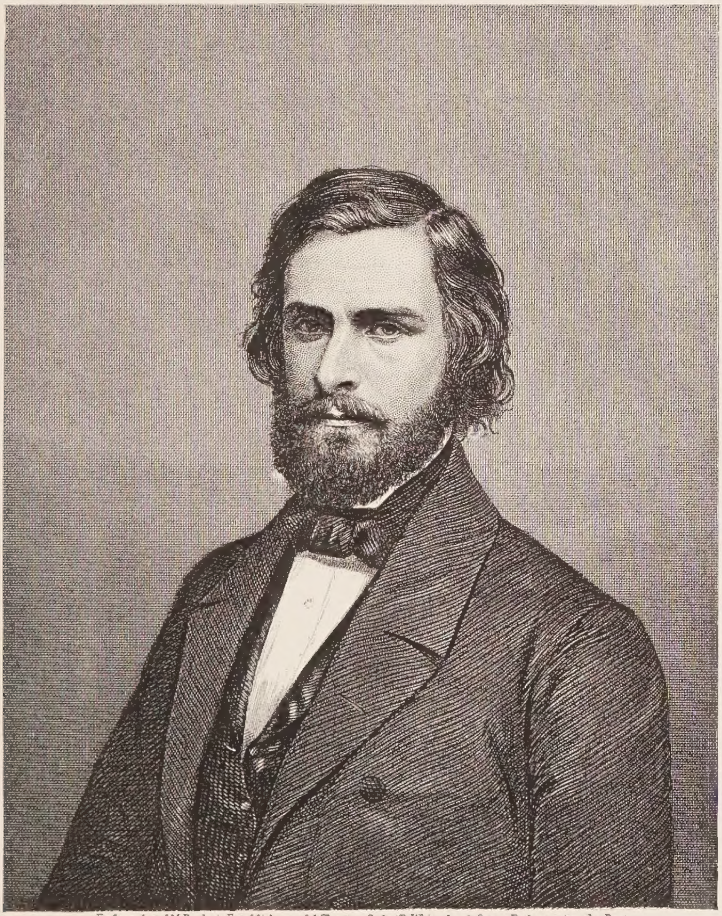
between it and specimens of *Trichina spiralis* which he had met with in several human subjects." A European helminthologist doubted the determination and reclassified it as *Trichina affinis* but twenty years later the world came back to Leidy's views. So it was elsewhere also. His sharp vision detected the eye in Balanus and his record led Darwin to look for it in other members of the order. In the monograph on *Fresh Water Rhizopods* Leidy refers to his observation in 1844 of the amoeboid movement of the white blood corpuscles later described (in 1846) by Wharton Jones. In a manner illustrating at once his loyalty and his modesty he often said that this discovery rightly belonged to American science.

But it would be wrong to leave the impression that his work was exclusively or even preeminently taxonomic and descriptive. While he sought patiently to determine the precise facts and to assemble them in systematic order, his mind was keenly alive to the importance of biological data. He rarely communicated to the Academy a description that he did not enrich by salient observations on habits and on relations to man and other animals. In his *Flora and Fauna Within Living Animals* he emphasized the radical changes in form and the other complexities associated with the life history of parasitic animals. Many of his early notes deal with stages in such life histories and his paper on *Nematoidea Imperfecta* relates in 1851 an early effort to determine experimentally the adult forms arising from such larval stages.

No one can scan even the titles of Leidy's publications without being struck by their unusually broad range as well as by the number of contributions he made to science. He was writing in the same year, and often in the same month, or even reporting at the same meeting of the academy, studies on fossil vertebrates, protozoa, insects, minerals, parasites, human anatomy, bacteria, cell structure, and transplanting cancer! A more careful analysis of these publications discloses the fact that they fall into rather distinct groups representing four main currents of interest and activity: microscopic anatomy, paleontology, protozoology and parasitology. Furthermore, these lines of interest were developed in large part successively rather than synchronously so that they characterize certain periods in his life, even though not exclusively limited to any single period.

PIONEER WORK IN PARASITOLOGY

During the first years of Leidy's work as a contributor to scientific literature he confined his attention practically exclusively to the study of the minute anatomy of lower invertebrates and the quality of his work is well exemplified by the comments of Binney on the plates and descriptive text which Leidy, then barely 21, contributed at the author's request to the well known work on Terrestrial Mollusks. Not until 1847 did he publish on paleontology and it was 1850 before studies on



Engraved at J.M. Butler's Establishment, 84 Chestnut St. by R. Whitechurch from a Daguerreotype, by Root.

Joseph Leidy

PROF. OF ANATOMY IN THE UNIVERSITY OF PENNA

PLATE II

fossils assume a prominent place in his writings. During this period his papers show increasing attention devoted to the study of parasitic forms. In 1851 he completed his *Flora and Fauna Within Living Animals,* and his standing as a parasitologist was assured even if he had never written another line on the subject. But neither the interest in this field nor his work on it was terminated here.

The series of studies on parasitology made in this first period of scientific activity was brought together in a synopsis published in 1856 and in a series of additions and corrections that appeared two years later. This was distinctly a pioneer work as nothing of its kind had been attempted in this country previously, and it has remained almost the only publication of the kind available up to within recent years. The paper, which was entitled *A Synopsis of Entozoa and Some of Their Ectocongeners,* lists 172 species of parasitic protozoa, trematodes, cestodes and nematodes, including many new genera and species. In conformity with the usual custom of the time the descriptions are very brief and consequently often difficult to evaluate rightly. But they represent for that day unusual knowledge of detailed structure and keen judgment on the significance of structural features. The synopsis embraced thus a wide range of material and morever represented the work of a single investigator. In both aspects it was unique when compared with European publications of somewhat similar character and date.

But the newly undertaken studies on fossil vertebrates began to crowd out microscopical investigations and for nearly twenty years Leidy worked and published chiefly on paleontology. However, beginning about 1872 he devoted his attention assiduously again to microscopic studies, first on protozoa which held him closely until 1876, and after that once more to parasitology, the field in which he was primarily engaged during the last years of his life.

These changes in Leidy's activity were largely determined by external conditions and a letter to Baird, dated Nov. 20, 1850, when Leidy had just returned from Europe, shows vividly how he was tempted away from his early microscopical studies. After discussing his researches on parasitic forms he comments on Baird's offer of fossils from the Bad Lands and adds:

"You mention to me the reception of mammalian fossils from the mauvaisses terres by the Smithsonian Institution and obligingly offer them to me for 'working up.'

"I am delighted with such an opportunity. If you will send them to me I will describe them immediately and prepare a memoir for the Smithsonian. I can readily do it as they are comparatively easy. I can lay a specimen down and return to it at a leisure moment. Not so with microscopic investigation; it requires length of time without interruption which I cannot have during the winter; send them to me immediately; good care will be taken of them."

From 1856 to 1870 Leidy published very little on helminthology and only a few notes on miscroscopic anatomy of other forms. But then the tide turned once more. How conditions changed and the old work was resumed is beautifully told by Sir Archibald Geikie (1892):

"I cherish as one of the most memorable incidents of a visit which I paid to Philadelphia in the year 1879 my meeting with this distinguished naturalist and most lovable man. With what modesty he spoke of his own work, with what generous appreciation he referred to that of others, with what infinite patience and gentleness he would unfold and explain his views to any questioner who seemed to be interested in them! I well remember the pathos of his remarks as he told me how he had been led to abandon his researches in vertebrate paleontology and return to his first love—the rhizopods, on which he published that same year a magnificent monograph. 'Formerly,' he said, 'every fossil bone found in the States came to me, for nobody else cared to study such things. But now Professors ——— and ———, with long purses, offer money for what used to come to me for nothing, and in that respect I cannot compete with them. So now, as I get nothing, I have gone back to my microscope and my rhizopods and make myself busy and happy with them.'"

ESTIMATES OF LEIDY'S WORK

Leidy's greatest work is recognized by all biographers as having been done in the field of vertebrate paleontology as shown in the number, breadth and accuracy of his studies, as well as in the splendid monographs of permanent value which he published in that field. And there is no reason to dissent from the view expressed by Geikie: "Dr. Leidy was universally acknowledged to be the Cuvier of American paleontology. And the praise lavished on him by his own fellow citizens was reechoed in no stinted measure in Europe." He was the first in the field and laid the foundations for the subsequent studies by a series of American investigators which have commanded the attention of scientific men both at home and abroad. The vast amount of paleontological material that was sent him between 1850 and 1860 drew his attention away from the studies he had so successfully inaugurated in other lines than this so that for nearly twenty years from 1856 to 1872 as already noted he published hardly more than a few brief notes in any other field. The splendid character of this work compels parasitologists to deplore the influences that drew him away from this earlier work and brings them to echo the remark of Kölliker to Leidy's nephew, "How I regret that your uncle ever saw a fossil bone."

To be sure, in this interval Leidy had published his text-book on human anatomy which is unexcelled in accuracy and clearness, and had also done splendid work as a surgeon in the Civil War, but after all these and certain other studies were but simple variations of the studies on gross anatomy which were incorporated in his paleontological contributions. About 1872 circumstances already noted carried him back to microscopic anatomy, his first love, and he spent several years in the study of the aquatic fauna which culminated in the appearance

of his monograph on fresh water rhizopods in 1879. This work was important for its bearing on parasitology as he was led to study carefully the protozoan parasites, particularly in various groups of insects. But it does not appear just to assign to his studies on protozoa, as some biographers have done, a place among his contributions to knowledge which is second only to his work on vertebrate paleontology. Yet an equitable judgment concerning his work on parasitology can be passed only after a more careful analysis of the extent and precise character of his writings.

Leidy's publications were numerous: the published record lists about 600 and some few items at least were omitted. Many of these are exceedingly brief,[2] being in fact only secretary's abstracts of oral discussions at the meetings of the Philadelphia Academy. Even these briefer notes are full of new information regarding structure, habits and relations and those bearing on helminthology and parasitology were in such constant demand that they were brought together and reprinted in 1904. They constitute the first and even yet the only extensive work in this field in America.

It is difficult to compare justly his work on parasitology with that in other lines. In number of titles it stands second to that in paleontology, and in major publications also. However, no single publication in parasitology achieved the perfection of his monograph on *Fresh Water Rhizopods* which stands today unexcelled in its field. On the other hand it is fair to say that the *Flora and Fauna Within Living Animals* was epoch-making in a sense that cannot be affirmed of any of his other writings outside the field of paleontology.

It has already been noted that Leidy's contributions to parasitology are pretty definitely limited to two periods in his career. Among the very first articles from his pen came two contributions to parasitology, one of which is the very important note on trichina to which more extended reference is made elsewhere. Between 1846 and 1858 he published some sixty notes and longer contributions in this field. Then for ten years one finds hardly a line on this subject. In 1870 contributions on parasitology began to appear again and are extended until in the last fifteen years of his life between 1876 and 1891 he contributed again about sixty papers on various topics in parasitology. He left an immense mass of unfinished material in the field, and as is well known, he had been planning for years the publication of an extended work on parasitology. Probably the most nearly completed of these unfinished

2. Osborn cites a fine comment by Calkins bearing on this point. "While these observations were made with keenness of perception, it must still be confessed that they were often expressed in quite too brief form for clear general understanding. In this he only followed the plan of his European contemporaries and while his ideas are distinct with the specimen itself in view, it is undoubtedly true that the originals must be worked over more fully."

items was a set of manuscript notes and drawings on gregarines which was later incorporated into Crawley's monograph on the polycystid gregarines of the United States. Of the new genera which Leidy described among living animals, more than half were published between 1846 and 1858, and nearly all of the rest after 1874.

It is important to note also the range of work which he did in the field of parasitology. This is indicated in the first period of research activity in that field by the character of the synopsis referred to. Among the publications published in the second period between 1886 and 1891 are longer contributions on the tapeworms of birds, parasites of shad and herring, of termites, and on leeches. Almost the last publications from his pen were an extended article on entozoa printed in November, 1890, which dealt with a variety of parasites from different hosts, and a second printed in April, 1891, which was almost equally varied. The material which was left unfinished included studies on gregarines already referred to and other notes and drawings brought together by Nolan in five volumes of Leidyana, which constitute a mine of information for future investigation.

During this second period of productive work in parasitology Leidy completed one important contribution that has been overlooked by many because of the manner in which it was published. In 1882 for the American edition of Holmes, *System of Surgery,* he revised articles on *Parasites and the Diseases They Produce,* and on *Venomous Insects and Reptiles,* which appear with notes and observations in Volume III. In 1888 he wrote a treatise on Intestinal Worms for Pepper's *System of Practical Medicine by American Authors.* This section, which covers thirty-five pages in the second volume, is the first comprehensive treatise on human parasites published on this continent.

DISCOVERY OF TRICHINA IN PORK

Among the very first of Leidy's contributions was a note recorded by the secretary of the Philadelphia Academy in October, 1846, as follows:

> Dr. Leidy stated that he had lately detected the existence of an Entozoon in the superficial part of the extensor muscles of the thigh of a hog. The Entozoon is a minute, coiled worm, contained in a cyst. The cysts are numerous, white oval in shape, of a gritty nature, and between the 30th and 40th of an inch in length.
>
> "The Entozoon he supposes to be the Trichina spiralis, heretofore considered as peculiar to the human species. He could perceive no distinction between it and the specimens of T. spiralis which he had met with in several human subjects in the dissecting rooms, where it had also been observed by others, since the attention of the scientific public had been directed to it by Mr. Hilton and Prof. Owen."

This has been regarded by some as Leidy's "most important practical contribution to helminthology" from the standpoint of public

health.[3] It is in fact a striking illustration of his keen scientific judgment and yet a closer analysis of the situation shows that the observation not only remained apparently unknown but was also without evident influence on European investigators, who were then engaged in an active controversy in their efforts to work out the life history of trichina and its relations to man. The case stands as follows: Leidy's record was copied in the Annals and Magazine of Natural History (1847) and incorporated by Diesing in his *Systema Helminthum* (1851) but the latter listed Leidy's find as a new species under the name *Trichina affinis,* grouping it with larval forms from a dozen other hosts, mostly birds. Several European writers cite the case under this new name, and no one under Leidy's original designation. Indeed Leidy was himself sufficiently impressed by the authority of Diesing that, without comment, in his *Synopsis of the Entozoa* (1856) he listed his form under Diesing's name and cited his own record as a synonym. But the forms which Diesing associated with Leidy's find are really Microfilariae and so unlike Trichina that if Leidy had known them at first hand he would have recognized the lack of relationship instantly. As the result of this misinterpretation and of scanty information regarding the discovery, Leuckart, Zenker, Virchow and others failed to mention it at all, or like Küchenmeister, utilized it to support the false [4] hypothesis that the encysted form in the pig was only the larval stage of the adult Trichocephalus in man.[5] In consequence, Leidy's observation failed to contribute to the elucidation of the problem, as it might well have done. In 1859 Leidy exhibited to the Philadelphia Academy specimens of a Trichina found in the muscles of a human subject and stated that he often met with the parasite. In the following year he reported Leuckart's experiments showing Trichina was not the immature stage of a Trichocephalus or Stronglus, as had previously been generally believed. In 1866, the records of the Academy contain this interesting note:

3. I am unable to verify the statement of Garrison that in 1848 Leidy was "already well known through his contributions to natural sciences, *particularly those on the Trichina.*" The statement is undoubtedly correct but the basis not well chosen as this particular item is almost unmentioned in European contemporaneous scientific literature and its deep significance nowhere recognized.

4. Küchenmeister (1855) says "glaube ich . . . dass die kaum beträchtlich grösser zu nennende *Trichina affinis* Diesing's, die Leidy in Philadelphia in den Extensoren des Schenkels eines Schweines fand, mit unserer *Trichina spiralis* identisch gewesen sein dürfte.

5. The only mention Leukart makes of Leidy's work in his monograph and in his *Menschliche Parasiten* falls in connection with the historical survey, where he explains the view long held that Trichina was the larval form of Trichocephalus and shows how Leidy's discovery was naturally enough utilized to support this view.

"In answer to a question from one of the members whether he had noticed Trichina in pork, Dr. L. observed that he had been the first to discover this parasite in the hog; the discovery having been made twenty years ago, as may be seen by referring to the Proceedings of this Academy for October, 1846, page 107-8. This notice had attracted the attention of the German helminthologist as proved by reference to Diesing's *Systema Helminthum,* vol. ii, pages 114, and Leuckart, *Untersuchungen über Trichina spiralis,* pages 6, 18.

"The circumstances under which the Trichina had been first detected in pork, was on an occasion when Dr. L. had dined on part of the infested meat. While eating a slice of pork, he noticed some minute specks, which recalled to mind the Trichina spots seen in the muscles of a human subject only a few days previously. Preserving the remainder of the slice, on examination of it microscopically he found it full of Trichına spiralis, but the parasites were all dead from the heat of cooking. In conclusion, Dr. L observed that all meats were liable to be infested with parasites, but that there was no danger from infection if the meats were thoroughly cooked, for he had satisfied himself by experiment that entozoa are destroyed when submitted to the temperature of boiling water."

Even as late as 1876 Leuckart made a serious error in stating "das von Leidy (1847) beobachtete Vorkommen eines als *Trichina affinis* beschriebenen Wurmes aus dem Muskelfleische des Schweines," whereas Leidy only adopted that erroneous designation in 1856 under the influence of the great Diesing, at that time the accepted authority in parasitology. It would look as if even at this late date Leuckart was not clear regarding the exact facts in the case since he writes in the very next paragraph to that cited above, "Braucht man doch nur annehmen, dass die *Trichina affinis* mit der *Trichina spiralis* identisch sei was nach den Mittheilungen Leidy's *trotz der abweichenden Benennung* keineswegs unwarscheinlich war." (Italics not in original.)

In 1880 Nolan stated in a sketch of Leidy that "Leuckart afterwards acknowledged he was indebted to this communication for his success in tracing the development of Trichina in the hog and man." This comment must have been known to the European investigators and remains uncontradicted so far as I can find. Yet, I cannot locate any such acknowledgement in Leuckart's writings. When Leidy's nephew was in Berlin in 1896 Virchow told him personally that he had had a lengthy correspondence with Leidy in 1849 and 1850 just after he began his studies in pathology. This correspondence on Leidy's discovery of Trichina in pork, as Virchow stated in the conversation, suggested to him (Virchow) and Leuckart the scheme of experimentation on the life cycle of the parasite. Yet so far as I can find Virchow nowhere mentions Leidy in this writings.

Looking backward one can see how the life history of Trichina might have been interpreted many years in advance of its actual solution if the correct observations of Leidy had been accepted. But in fact, even the German investigators who knew of his work gave it no adequate consideration and many years elapsed before they came back by another route to the conception that the hog and man acted both equally as hosts for the parasites.

This episode illustrates both the critical insight of the man and also his clear appreciation of the proper method for handling the danger, for as Leidy correctly stated in 1866, thorough cooking eliminates danger from infection by parasites. Even yet the world has not come to unanimous acceptance of this simple and universally successful method for preventing trichinosis, which he advocated. The case also illustrates Leidy's dislike of controversy for when his friends urged him to assert his part in the work and the importance of his discovery, he only replied that the discovery was merely one episode in his life and "the important thing is that the discovery or fact should be made known. It is of little consequence who made it." To him also controversy meant a "disturbance of that peace of mind" which was most distasteful and also interfered sadly with his researches.

SOME IMPORTANT OBSERVATIONS ON PARASITES

By virtue of the fact that Leidy was a pioneer in this field of work in America and that he was relied upon everywhere to furnish an explanation for the problems which were encountered, he was in receipt of material of the most varied type from all parts of the country and even from the Orient; thus, Dr. J. G. Kerr, one of the earliest missionaries in China, distinguished for his medical work, sent to Leidy in 1873 specimens of the intestinal fluke common there. It is not strange that at that date he confused the specimen with the liver fluke which is common here in cattle and sheep. This error he found and rectified later. Leidy not only recorded one of the very first occurrences of many important parasites, especially those of man; he also recognized promptly the significance of their presence, and put on record for the guidance of others interpretations which are of marked significance in view of the limited knowledge concerning these forms current at that time. This was clearly shown in this original record of presence of trichina in the hog already discussed. In 1878 he discussed the distribution and frequence of the two human tapeworms, and was the first to show that contrary to the ordinarily accepted belief, *Taenia saginata* was much more common than the pork tapeworm, *Taenia solium*. He notes in connection with this case the fact of evident significance that the carrier of the specimen "had been in the habit of eating raw buffalo meat." It is evidently possible that this was a specimen of some now exceedingly rare species rather than that to which he referred it, for as has been pointed out by several recent students, the native herbivores of North America may have sheltered species of tapeworm closely allied to but not identical to those reported from the old world. Isolated specimens which lend color to such a view have been described under different names (*Taenia confusa* and *Taenia abietina*); but be that as it may, Leidy recognized instantly the bear-

ing of the patient's diet on the problem of his infestation with the tapeworm. In 1879 Leidy reported specimens of the fish tapeworm, *Dibothriocephalus latus,* which had come from a native of Sweden that had been in the country only a few months. They were the first of the species which Leidy had seen in a host living in this country. In 1884 Leidy called attention to specimens of *Taenia flavopunctata,* now better known as *Hymenolepis diminuta.* These came from a child only three years of age and the species had been observed but once previously. Leidy pointed out definitely the probability that the worm is more common than might be inferred from cases on record. He further suggested that it has probably escaped notice from its diminutive size and from lack of knowledge of tapeworms in general. The more recent studies of Ransom on this species have abundantly justified Leidy's prediction made thirty years before. In 1886, writing on parasitic worms, Leidy recorded the discovery in the cat of a form which he listed under the name *Ancylostoma duodenale.* It is true that in all probability he had not the species named but a closely related one that is often parasitic in the cat. This does not in the least affect his general conclusion that the discovery indicates the probability that it also infests man and is one of the previously unrecognized causes of pernicious anemia. It was many years later that the well known and important work of Ashford, Stiles and others, disclosed the full significance for the human species on this continent of the hookworm and associated anemia.

Leidy's faculty to draw correct inferences from his observations and to apply them for the guidance of men is illustrated by many simple suggestions that were appended to his discussions of unusual and important parasites. They are handled so naturally that the careless observer might regard them as casual observations or after thoughts, but this can hardly suffice to explain their frequence and value. As early as 1853 he wrote, "Cooking food is of advantage in destroying the germs of parasites, and hence man, notwithstanding his liability to the latter, is less infested than most other mammalia." In 1878 when reporting on parasites received from physicians who expressed apprehension about them and thought they had traced several cases of illness to the use of food infested with worms, Leidy in discussing the particular situation observed that as already well known to naturalists most animals are infested with parasites which are transmitted in feeding. "The remedy against transmission was heat. He who uses only well cooked foods need have no apprehension from such foods." Or again as he said in March, 1866, when discussing trichina, "All meats were liable to be infested with parasites, but there was no danger from infection if the meats were thoroughly cooked, for he had satisfied himself by experiment that entozoa are destroyed when brought to the temperature of boiling water."

Philad^a.
Oct. 4, 1851

Prof. J. W. Bailey,

Dear Sir,

I was pleased to hear you have been helminthizing in the forests of Julus. I am now engaged in writing an extended memoir upon the flora and fauna of some of our animals which will be published by the Smithsonian Institution with numerous figures.

Within Julus marginatus there are three distinct nematoid worms: Ascaris infecta the largest, and Streptostoma agile with a very long apiculate tail and strongly annulated:

and Thelastoma attenuatum very much like the last but with a long cylindrical oesophagus instead of pyriform and a shorter tail —

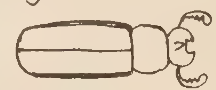
The entophyte is my Enterobryus elegans. You ask whether it is a plant or an animal. I think the former for these reasons:

1st It is a long closed organic cell, attached by a solid pedicle, and increasing by division at the free end, growing entirely by endosmosis, as in the case of all algae.

2nd Although movements are no indication of animality, yet all animals exhibit, at most periods of their life, movements. Enterobryus never has the slightest power of movement, except possibly in the spore which I have not been able to discover, although this would not indicate it to be an animal any more than the self moving spores of Achlya or Vaucheria prove them to be such.

If you wish to explore further you will find a most extraordinary profusion of life vegetable and animal within the ventriculus of Passalus cornutus, a common coleopterous insect, found in almost every decaying stump.

It is about an inch long with a horn upon its head. Black and shining ——



My notes on entophyta, published in the Proc. Acad. Nat. Sc. I will send to you shortly.

I would be very glad to see these entozoa from the Alligator, or any others you may meet with.

When an opportunity offers please send them directed to the Acad. of Nat. Sciences. Broad & George Sts.

Respectfully I subscribe myself
Joseph Leidy.

PLATE III

Another simple illustration will suffice to elucidate this characteristic. In November, 1871, he discussed flies as a means of communicating contagious diseases and stated that on the basis of his observations during the Civil War in a large military hospital where gangrene existed he believed that flies should be excluded from contact with the wounded. Recently he had found some flies that when caught and examined were swarming with spores of a fungus on which they had just fed. In view of the apparent ease with which he found a reasonable solution to most of the problems which presented themselves it is interesting to note his comment on the occurrence of a reputed tapeworm in a cucumber, concerning which he writes, "It cannot be admitted that the worm belonged to the cucumber, nor is it clear how it reached this position."

LEIDY'S MASTER WORK IN PARASITOLOGY

Leidy's most influential publication on parasitology was, in my opinion, *A Flora and Fauna Within Living Animals,* accepted for publication in December, 1851, and printed in the Smithsonian Contributions to Knowledge in 1853. The article is not large as it covers only 67 pages. It is, however, beautifully illustrated by ten plates and handles in a powerful manner not only the scientific facts observed, but the general discussion of their bearing on important general problems. In an intensive study of the intestinal canal of a myriapod and a beetle, Leidy demonstrated the occurrence of a typical flora and fauna which was both rich and varied.[6] His anatomical descriptions and illustrations are unsurpassed in their clarity and exactitude and are unequalled in the literature of the time. He did not content himself with a description of structure but worked out the development of the parasites and their relation to the organs of the host in which they occurred. He contrasted further the true plant parasites with the pseudo-entophytes which he encountered. It is in his general discussion that one finds after all the most striking evidences of the unusual character of this contribution. To judge the situation rightly, one must keep in mind the fact that this paper was written before the epoch making investigations of Pasteur, Tyndall and others had established on a firm foundation present day conceptions with reference to the origin of living organisms. The doctrine of equivocal or spontaneous generation was

6. Even earlier than this in his *Researches in Helminthology* (1849) he wrote "I have found numerous free or floating entophyta in the contents usually in the posterior part of the alimentary canal in mammals, aves, reptilia, pisces, mollusca, etc." This is, I think, the earliest demonstration of the bacterial flora of the intestine, and it was certainly thoroughly followed out and firmly established by the range of hosts he cited from almost the entire animal kingdom. I am informed that these views are more fully elaborated in his yet unpublished personal correspondence with Baird.

widely held and vigorously supported by men of high rank in scientific circles. To be sure it had lost the crude form in which it had been stated by students of medieval times and earlier days, but it was accepted with reference to the simplest microscopic organisms all the more generally because the very arguments that had disproved the possibility of its occurrence among complicated organisms lent color to the likelihood of its being found among those of the simplest type. The entozoa had always furnished the strongest support for the theory, and the complexity of their development, which had in large part eluded the efforts of investigators, gave additional weight to the view that these organisms arose *de novo* where they were discovered.

In the beginning of this paper Leidy says, "The very great majority of modern observations indicate that entozoa and entophyta are produced from germs derived from parents and have a cyclical development." To the readers of those days such phrases did not carry the demonstrative character that they present to modern students. It was a distinct challenge to the advocates of spontaneous generation. After reviewing the difficulties due to the fact that entozoa pass various stages of existence under totally different circumstances and undergo pronounced modifications in form such that successive stages cannot be recognized as such without further evidence, Leidy denies the necessity of spontaneous generation and challenges the supporters of the doctrine to present one single direct observation to substantiate it. His review of the general conditions of the earth and the phenomena of life in its relation to environmental factors is in general terms almost the same as that given by Huxley fully twenty years later. Many of the statements and the entire line of explanation anticipated in a definite way the views which in greater fullness found their expression eight years later in Darwin's Origin of Species. He refers to his own repetition of the experiments made by Schulze to test the possibility of spontaneous generation, and while acknowledging that negative results may not be conclusive, he states, "Be this as it may, the most prolonged and the most carefully conducted experiments have not led to the proof of a single instance of equivocal or spontaneous generation, even among the simplest of all living beings: but on the contrary that all lead further and further from or entirely disproved it." He then considers the factors concerned in the development of parasitic life and the relative abundance of parasites among animals of different habitats. In his discussion of the influence of parasites on the production of diseases, occurs a statement that has sometimes been misconstrued. He wrote, "That malaria and epidemic fevers have their origin in cryptogamic vegetables or spores requires yet a single proof. He was referring to "an ingenious little work by my distinguished friend, Dr. J. K. Mitchell on the cryptogamous origin of malarious and epidemic fevers." This

statement has been interpreted as indicating that Leidy "discussed the cause of malaria and wrongly construed that it was not of parasitic origin." The examination of the context shows that in the first half of the same sentence he acknowledges the agency of entophyta in the production of certain diseases and in the following sentence refers to the fact that "vegetables or spores conveyed through the air and introduced into the body through respiration could be detected," as indeed he himself had done in this very work while tracing the origin and development of the enteric flora which he described.

Leidy closed this general section of his paper with a list of described species of parasitic plants and animals to which man is subject. The thoroughness with which he has here demonstrated the origin and development of so varied a flora and fauna within the animals he studied was in a positive and convincing fashion an argument against the doctrine of spontaneous generation quite as powerful to many minds as the later experiments of the European investigators. In any event the work was read and quoted generally among European investigators and elicited everywhere outspoken praise.[7]

It is important to note that Leidy's critique of the theory of spontaneous generation was preeminently that of a biologist and included arguments that even Pasteur could not have formulated. In a footnote, for example, he writes:

> "The experiments of Crosse and Weeks appear to me exceedingly absurd; for, in the first case, how were the carbon and nitrogen of the animal body to be derived by the play of a voltaic current upon a solution of silicate or potassa? If they previously existed in the water, was it not quite as probable that the ova of Acari were there also? Again, when the solution of ferrocyanide of potassium was made the womb of life by the electrical current, why could not the embryology of the new being be observed? An Acarus is a highly complex animal, presenting a well-developed tegumentary, muscular, and nervous system, and a digestive, respiratory, and generative apparatus. The gap between the inorganic world and the Acarus is greater than that between the latter and man."

It was this paper *inter alia* that almost prevented his election to the chair of Anatomy at the University of Pennsylvania in 1853 as he was charged with attempting to overthrow the Mosaic record of creation through his geological teachings and his *attack upon spontaneous generation!*

CONCLUSION

A detailed study of his writings justifies the statement that no one has yet adequately presented or fully elucidated Leidy's contributions to helminthology and his writings will furnish rich leads to many future

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7. Professor Henry, Secretary of the Smithsonian Institution, sums up his report on this publication with these words: "the whole forming the most remarkable paper on physiology which has ever been produced by one of our countrymen."

workers in this field. How monumental the task of preparing a record of the full life work of this extraordinary man who in the same breath as it were, in a single letter records discoveries of far reaching import on bacteria, amoebae, worms, and fossil elephants.

Many biographical sketches, especially those written by his associates in the Philadelphia Academy, show that in the later years of his life Leidy had in mind the publication of an extensive work on parasitology [8] and the articles he published in those years dealt preeminently with that topic. All must regret that this project remained unrealized for he left a vast amount of unpublished data in this field and of this only a small part, that on Gregarinida, has been in shape for later publication. Fortunately his nephew brought together all of his writings on parasitology and they were reprinted in 1904 by the Smithsonian Institution under the title of Researches in Helminthology and Parasitology.[9] One must regret that these notes had not been rewritten by the master mind and his later studies incorporated. But even though the earlier items have an archaic cast and the work suffers from its natural discontinuity, yet it is a mine of information on American parasitology which even yet is far from worked out and will always be indispensible to investigators in this field. Despite all the defects incident to such a compilation it is a monument to the industry and ability of the author and foreshadows the monograph he had in mind but was not able to complete.

Henry B. Ward.

ILLUSTRATIONS

Plate I

Frontispiece.—Portrait of Leidy taken in 1883 when he was 60 years of age.

Plate II

Facing page 8. Copy of steel engraving representing Leidy at 28; taken in 1851, the year in which he completed his Flora and Fauna within Living Animals.

Plate III

Facsimile of letter in Leidy's handwriting (⅔ natural size); on page 17.

Professor J. W. Bailey to whom this letter was written was a distinguished member of the faculty at West Point Military Academy from 1838 to 1857. His scientific reputation was achieved principally by his researches in microscopy in which field he was a pioneer in the United States.

8. See Sketch of Joseph Leidy by E. J. Nolan (1889).
9. Smithsonian Misc. Collect., Vol. 46; 281 pp. No. 1477, 1904.

MICROSPORIDIAN PARASITES OF EPHEMERID NYMPHS *

R. Kudo

In an earlier paper (1921), I reported a microsporidian, *Nosema baetis,* parasitic in the nymphs of *Baetis* sp., observed in 1919 at Urbana, Illinois, together with a brief reference to the seven known species of Microsporidia parasitic in Ephemeridae of Europe and of South America. In the summer of 1920, I had opportunities of studying two hitherto undescribed species of Microsporidia in the nymphs of *Ameletus ludeus* and *Baetis pygmata* (?). The present paper deals with the brief description of these two forms. I am greatly indebted to Professor Charles P. Alexander of the Massachusetts Agricultural College for the identification of the host insects.

Thelohania mutabilis nov. spec.

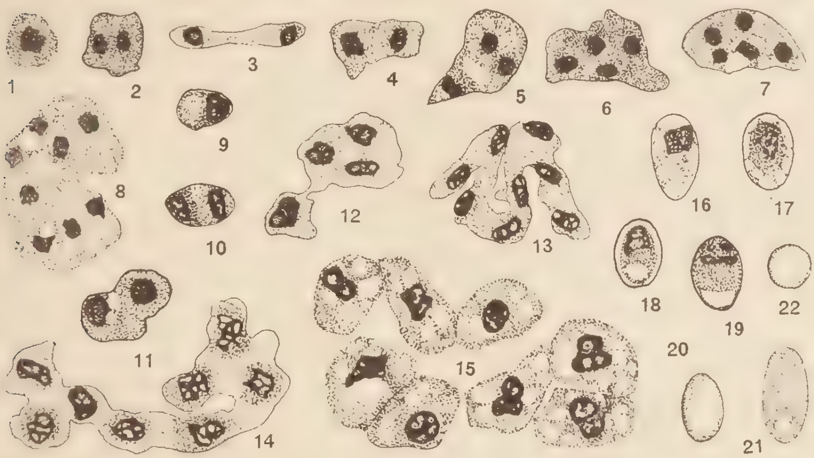
This microsporidian was found to infect the adipose tissue of the nymph of *Ameletus ludeus* Needham at Warren, Pennsylvania, in July, 1920. The host insects were collected from a small overflow stream of a spring in the woods. Four out of thirty-two host nymphs examined, were parasitised by the microsporidian. Contrary to the case of infection by *Nosema baetis* (Kudo, 1921), the host nymphs did not show any noticeable decrease in activity due to the infection, although slight opaque coloration was recognized in the infected area of the body.

Schizogony and sporogony appear to take place in ways similar to those of *Thelohania magna* (Kudo, 1921). Young schizonts are uninucleate rounded bodies and are found in the cytoplasm of the host cells. They multiply by binary fission or by multiple division, producing two, four or eight daughter individuals. The division seems to be repeated. The nucleus is compact and its division appears to be amitotic. Each schizont grows into a larger body, a sporont, whose nucleus becomes vesicular. The sporont further grows and the nucleus divides three times, forming eight sporoblasts in it. There seems to be considerable variation in the size of the sporonts at the end of sporoblast formation. Occasionally one finds tetrasporoblastic sporonts which undoubtedly give rise to larger sporoblasts, but octosporoblastic sporonts predominate in number over the former.

The spore is oval, elongated ovoid or pyriform in form. It is circular in optical cross-section. The spores are less refractive than those of *Nosema bombycis, N. apis* or *Thelohania baetica.* In the fresh

* Contribution from the Zoological Laboratory of the University of Illinois. No. 224.

state, some spores are filled with a finely granulated contents, while others show a small rounded clear space at one of the extremities. When stained, it becomes clear that the structure of the spore is similar to that of *Nosema baetis*. Size varies considerably. Fresh spores measure 3.8 to 5.5μ long by 2.5 to 3μ broad. The length of polar filament extruded under mechanical pressure is 70μ on an average.



Thelohania mutabilis nov. spec. Figs. 1-8, stages in schizogony; 9-15, stages in sporogony; 16-19, stages in development of spores; 20-21, fresh spores; 22, optical cross-section of spore. $\times$ about 2400.

Thelohania baetica nov. spec. Figs. 23-31, schizogonic multiplication; 32-38, sporogony; 39-41, fresh spores; 42, spore stained deeply with hematoxylin; 43, optical cross-section of spore. $\times$ about 2400; except fig. 42, $\times$ 3200.

Thelohania baetica nov. spec.

The microsporidian infects the adipose tissue of the nymphs of *Baetis pygmata* Hagen (?) collected at Spring Valley, New York, in August, 1920. Twenty-six nymphs were examined in fresh smears

and thirty-one were studied in section preparations. Of these, five were found to be infected by this parasite. No particular coloration nor decrease in activity of the infected host insects was noticeable. The infection was light, yet the nucleus of the host cells showed a hypertrophied condition as is ordinarily the case with microsporidian infections.

The schizogony and sporogony seem to be on the whole similar to those of *Thelohania magna*. Octosporoblastic sporonts were found exclusively. The peculiar characteristic of the present form is that the nucleus is relatively large throughout different stages of schizogony and sporogony. In the schizogonic division, nuclear material becomes divided into two groups, each being composed of two deeply staining bodies. Two fine chromatic filaments are frequently to be seen connecting the two groups of chromatic masses at the poles of the schizont. The nuclear division during the course of sporogony seems to be direct.

The spore is oval in form and highly refractive. Spore membrane is comparatively thick. The contents are finely granulated and occupy the entire intrasporal cavity except a place near one end, where crescent-shaped clear space is observable. The contents stain very deeply, while the clear space at one end remains unstained. The polar filament appears to penetrate through this space and is directly connected with the spore membrane. Dimensions are constant. Fresh spores measure 4 to 4.5μ long by 2.5μ broad. The extruded polar filament reaches 100μ in length.

Although no Microsporidia belonging to the genus Thelohania have been reported to occur in ephemerid nymphs (Kudo, 1921), reference must be made to *Stempellia mutabilis*. This microsporidian, according to Léger and Hesse (1910) was found parasitic in the fat bodies of *Ephemera vulgata* in France, and exhibits a mictosporous character; i. e., a sporont may produce one, two, four or eight sporoblasts (and ultimately spores). The spores vary therefore considerably both in dimensions (2 to 6μ) and in form from pyriform to ovoid. Monosporous or disporoblastic sporonts have so far not been found in *Thelohania mutabilis*. While the size of spores in the two species under consideration seems to show a similar variation, the range of variation of the American form is smaller than the French form. Hence I maintain that these two forms are not identical.

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TRANSMISSION EXPERIMENTS ON THE SPECIFICITY OF *HERPETOMONAS MUSCAE-DOMESTICAE* IN MUSCOID FLIES *

ELERY R. BECKER

The large number of protozoan parasites which have been given specific names that refer to their animal hosts indicates the strong belief of parasitologists in host specificity. In many instances the results of morphological and experimental investigation have justified such a belief. The recent careful morphological studies of Simon (1922) and Hegner (1922), as well as the earlier studies of Kofoid and his co-workers, show that the species of Giardia living in man, meadow mice, rats, dogs, and rabbits are distinguishable. The feeding experiments of Simon (1922) suggest a rigid host specificity for Giardia. Failure to find animal reservoirs for human infections with Giardia, *Endamoeba histolytica*, and the three forms of human malaria have somewhat intensified the general belief in absolute host specificity.

The workers who have investigated the flagellate parasites of the non-biting muscoid flies have, as Alexeiff (1913a) pointed out, assumed that a Herpetomonas found in a host where it had not previously been noted is a new species. The result is that the literature contains descriptions of a large number of species of Herpetomonas which are hardly distinguishable. Alexeieff (1913b) lists as synonyms of *Herpetomonas muscae-domesticae, Leptomonas drosophilae* Chatton and Alilaire, *L. pycnosomae* Roubaud, *L. ampelophilae* Chatton and A. Leger, and *Herpetomonas luciliae*, Strickland. To his list I should add *H. calliphorae* Swingle, *H. sarcophagae* Prowazek, and *H. homalomyiae* Brug. In his various writings Patton has avoided the common error by noting that *Herpetomonas muscae-domesticae* may be present in a number of species of hosts.

Alexeieff (1913b) justified his grouping of a large number of supposed species of *Herpetomonas* into three species on strictly morphological grounds. He argues that, since in the protozoa we can neither apply the specific test of cross fertilization nor use the delicate cultural reactions upon which bacteriologists depend, we must use morphological criteria alone in classifying protozoa. He further makes

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* From the Department of Medical Zoology, School of Hygiene and Public Health, Johns Hopkins University. This paper is the third of a series concerning the hemoflagellates living in the intestines of insects. The writer is indebted to Drs. R. W. Hegner and W. H. Taliaferro for many helpful suggestions and criticisms. Thanks are due to Dr. F. M. Root for identifying the species of flies for me and for his friendly interest in the fly infection experiments.

the debatable statement that physiological differences of specific importance between organisms have their recoil in the morphology.

It was for the purpose of determining how far Alexeieff's assumption of the identity of a number of the *Herpetomonas* entozoic in the common non-biting muscoid flies, based upon morphological grounds, would be substantiated by cross infection experiments, that these experiments were undertaken. To state the problem in a question—if the type of Herpetomonas known as *Herpetomonas muscae-damesticae* is morphologically alike in a number of different species of hosts, might there not be physiological differences which have not manifested themselves in the morphology of the flagellate markedly enough to be detectable, yet of sufficient importance to render the parasite incapable of living, multiplying, and establishing a normal infection in any species of host other than that in which it is found in nature?

An examination of a large number of "wild" flies captured during the summer of 1922 showed that flagellates of the type described by Prowazek (1904) as *Herpetomonas muscae-domesticae* may be present in a number of species of hosts. This flagellate may be found naturally in *Phormia regina, Lucilia sericata, Musca domestica, Cochliomyia macellaria, Calliphora erythrocephala,* and *Sarcophaga bullata.* Sixty-six per cent. of *Phormia reginia* were found to be infected, but not over two or three per cent. of *Musca domestica,* although a record of the incidence of infection of the latter species was not kept.

The question may be raised as to whether the herpetomonads of these various species of flies are similar enough morphologically to be considered a single species. After studying a number of slides of the parasite from each species of host, it soon became evident that whether one or several species were represented, it was impossible to make any distinctions of specific importance. It is *Herpetomonas muscae-domesticae* which Prowazek (1904) incorrectly described as a biflagellate, because of its tendency to continue in a state of division, with which we are concerned here. It has the prominent marginal granules, basal granules, deep staining parabasal body, and vesicular nucleus with a thin achromatinic nuclear membrane. As was noted in a previous paper (Becker, 1923), two other types of Herpetomonas may be found in muscoid flies. The one is smaller than *H. muscae-domesticae,* does not exhibit the almost constant biflagellated appearance, and has no visible marginal granules. It is probably the same as *"Crithidia" calliphorae* Swellengrebel. The other type, like *H. muscae-domesticae,* shows a tendency toward the biflagellated division condition, has visible marginal and basal granules, but differs from *H. muscae-domesticae* in that it has a nucleus with a pronounced achromatinic nuclear membrane and a small central karyosome. But in regard to the

H. muscae-domesticae type, all must accept Alexeieff's opinion that this morphological type of flagellate occurs in a number of different species of hosts.

In order to determine whether or not the flagellates entozoic in the alimentary canal of a fly of one species may possess physiological characteristics which make it incapable of carrying on its vital activities in the alimentary canal of a host of a closely related species, and incapable of producing there a natural infection, certain factors are necessary.

First, naturally infected flies ("wild" flies) must be available.

Second, the flies to be tested for their susceptibility to parasites taken from hosts of another species must be "clean"; i. e., it must be definitely known that these flies are not already infected at the beginning of the experiment and that they are not exposed to accidental contamination after the time of intentional inoculation.

Third, the nature of the infection produced in the artificially infected flies must not be unlike that found in "wild" flies; i. e., the parasites inoculated *per os* into the new host must establish themselves in the alimentary canal, multiply, produce the same stages in their life history as in the host in which they were naturally found, and these parasites must be infective to other "clean" flies under conditions simulating those in nature.

"Wild" infected flies of the species noted above were generally obtained by trapping, but in some cases the fly swatter was resorted to. "Clean" adult flies (except *Musca domestica*) were raised from the eggs in the laboratory by the method described in a previous paper (Becker, 1923). These flies belonged to the same species as the "wild" flies found to be infected with flagellates of the *H. muscae-domesticae* type; viz., *Phormia regina, Lucilia sericata, Calliphora erythrocephala, Sarcophaga bullata,* and *Cochliomyia macellaria. Musca domestica* was raised from larvae collected from horse manure. Sixty such larvae were examined for Herpetomonas and found to be negative. Adults examined immediately after hatching and one to two weeks after hatching were always found to be free from flagellates, as were the controls to be mentioned later. It is necessary to emphasize the fact that in this case the larvae and adults raised from the uninfected larvae were negative for Herpetomonas, because Patton (1921) recently discovered that the larvae of *Musca nebulo* were infected with a Herpetomonas which persisted through the pupa to the adult. The freedom of *Musca domestica larvae* from Herpetomonas infection in the vicinity of Baltimore may be explained by the low incidence of infection of the adults, not over three present at most. As will be shown later, it is possible that even the adults get their infections from flies of other species. Immediately after hatching the adult flies were chloroformed and put

into sterile glass jars covered with sterile cheese-cloth. For each species of "clean" fly there were seven containers, six of them to be used in the infection experiments and the seventh for a control.

The method of conducting the experiment was as follows. The flies were fed dilute cane sugar solution made slightly alkaline (Ph 8) until within twenty-four hours of the time when they were to be given an infected meal. After twenty-four hours of starvation the flies were given a meal consisting of a few drops of 0.4 saline solution in which had been emulsified part of the contents of an intestine heavily infected with Herptomonas. After the time of inoculation *per os* the only food of the fly consisted of the dilute sugar solution. The alimentary canals of the inoculated flies were removed and examined microscopically for Herpetomonas from one to two weeks after the time of feeding the infected material. The following summary outlines briefly the important details and results of the experiments. The numbers of infected and unifected flies are based upon the flies remaining alive, since many of the flies died and dried up during the interval between inoculation and examination.

1. Infection experiments with *Musca domestica,* hatched July 23:

A. 1. Fed Herpetomonas from *Phormia regina* July 25. Examined for parasites August 5. Negative 4. Heavily infected 5.* Lightly infected 4.*

2. Fed Herpetomonas from *Lucilia sericata* July 24. Examined for parasites August 5. Negative 1. Heavily infected 7. Lightly infected 3.

3. Fed Herpetomonas from *Calliphora erythrocephala* July 27. Examined for parasites August 5. Negative 4. Heavily infected 5. Lightly infected 6.

4. Fed Herpetomonas from *Cochliomyia macellaria* July 27. Examined for parasites August 5. Negative 0. Heavily infected 10. Lightly infected 1.

5. Fed Herpetomonas from *Sarcophaga bullata* July 26. Examined for parasites August 5. Negative 2. Heavily infected 2. Lightly infected 5.

B. Controls—Examined for parasites August 5. Negative 16. Positive 0.

2. Infection experiments with *Phormia regina,* hatched August 1:

A. 1. Fed Herpetomonas from *Musca domestica* August 2. Examined for parasites August 11. Negative 1. Heavily infected 6. Lightly infected 2.

2. Fed Herpetomonas from *Lucilia sericata* August 2. Examined for parasites August 11. Negative 4. Heavily infected 6. Lightly infected 7.

3. Fed Herpetomonas from *Calliphora erythrocephala* August 2. Examined for parasites August 11. Negative 4. Heavily infected 7. Lightly infected 4.

4. Fed Herpetomonas from *Cochliomyia macellaria* August 2. Examined for parasites August 11. Negative 4. Heavily infected 6. Lightly infected 4.

5. Fed Herpetomonas from *Sarcophaga bullata* August 2. Examined for parasites August 11. Negative 2. Heavily infected 8. Lightly infected 4.

B. Controls—Examined for parasites August 11. Negative 17. Positive 0.

3. Infection experiments with *Lucilia sericata,* hatched July 26:

A. 1. Fed Herpetomonas from *Phormia regina* July 27. Examined for parasites August 5. Negative 0. Heavily infected 15. Lightly infected 1.

2. Fed Herpetomonas from *Musca domestica* July 28. Examined for parasites August 5. Negative 2. Heavily infected 7. Lightly infected 3.

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* Heavily infected means that the alimentary canal of the fly was literally filled with the flagellates. Lightly infected may mean anything from the condition where the flagellates are somewhat less in numbers to the condition where very few are present.

3. Fed Herpetomonas from *Calliphora erythrocephala* July 27. Examined for parasites August 5. Negative 2. Heavily infected 6. Lightly infected 7.

4. Fed Herpetomonas from *Cochliomyia macellaria* July 27. Examined for parasites August 5. Negative 0. Heavily infected 3. Lightly infected 2.

5. Fed Herpetomonas from *Sarcophaga bullata* July 27. Examined for parasites August 5. Negative 3. Lightly infected 4.

B. Controls—Examined for parasites August 5. Negative 23. Positive 0.

4. Infection experiments with *Calliphora erythrocephala,* hatched August 3:

A. 1. Fed Herpetomonas from *Lucilia sericata* August 7. Examined for parasites August 17. Negative 4. Heavily infected 1.

2. Fed Herpetomonas from *Phormia regina* August 7. Examined for parasites August 17. Negative 4. Heavily infected 1. Lightly infected 2.

3. Fed Herpetomonas from *Musca domestica* August 7. Examined for parasites August 17. Negative 5. Lightly infected 2.

4. Fed Herpetomonas from *Cochliomyia macellaria* August 7. Examined for parasites August 17. Negative 5. Lightly infected 1.

5. Fed Herpetomonas from *Sarcophaga bullata* August 7. Examined for parasites August 17. Negative 4. Heavily infected 3. Lightly infected 1.

B. Controls—Examined for parasites August 17. Negative 14. Positive 0.

5. Infection experiments with *Cochliomyia macellaria,* hatched August 1:

A. 1. Fed Herpetomonas from *Calliphora erythrocephala* August 2. Examined for parasites August 11. Negative 4. Lightly infected 3.

2. Fed Herpetomonas from *Lucilia sericata* August 2. Examined for parasites August 11. Negative 7. Lightly infected 3.

3. Fed Herpetomonas from *Phormia regina* August 2. Examined for parasites August 11. Negative 6. Slightly infected 2.

4. Fed Herpetomonas from *Musca domestica* August 2. Examined for parasites August 11. Negative 4. Heavily infected 4. Lightly infected 4.

5. Fed Herpetomonas from *Sarcophaga bullata* August 2. Examined for parasites August 11. Negative 4. Heavily infected 2. Lightly infected 2.

B. Controls—Examined for parasites August 11. Negative 10. Positive 0.

6. Infection experiments with *Sarcophaga bullata,* hatched August 8:

A. 1. Fed Herpetomonas from *Cochliomyia macellaria* August 9. Examined for parasites August 21. Negative 4. Heavily infected 2. Lightly infected 2.

2. Fed Herpetomonas from *Calliphora erythrocephala* August 9. Examined for parasites August 21. Negative 5. Heavily infected 2. Lightly infected 4.

3. Fed Herpetomonas from *Lucilia sericata* August 9. Examined for parasites August 21. Negative 4. Heavily infected 4. Lightly infected 6.

4. Fed Herpetomonas from *Phormia regina* August 9. Examined for parasites August 21. Negative 3. Heavily infected 3. Lightly infected 1.

5. Fed Herpetomonas from *Musca domestica* August 9. Examined for parasites August 21. Negative 4. Heavily infected 2. Lightly infected 1.

B. Controls—Examined for parasites August 11. Negative 12. Positive 0.

In addition to these experiments a number of laboratory bred flies belonging to the species *Morellia micans* and *Sarcophaga securifera* were fed Herpetomonas from *Lucilia sericata.* An examination made nine days later showed that out of nine of the former, one was infected; and out of fourteen of the latter, two were infected. Unfortunately no controls were kept. It might be well also to mention here that attempts to infect Phormia, Lucilia and Musca flies with *Herpetomonas* from *Drosophila melanogaster* were unsuccessful. Likewise, attempts to infect *Drosophila melanogaster* with *Herpetomonas* from *Phormia regina* were unsuccessful. The experiment needs to be repeated.

The results of these experiments indicate very plainly that the *Herpetomonas* which occurs naturally in the six species of muscoid flies mentioned above is non-specific for its host to the extent that parasites from any one of the hosts can produce an infection in the other five. In many of the infections noted as heavy, the flagellates were as numerous as in the heaviest infections found in nature, in which the intestine is literally blocked with its inhabitants. So far as could be ascertained, the same stages in the life history were found in the inoculated flies as are found in naturally infected "wild" flies; viz., the adult flagellate, the trypaniform, the cyst, and dividing stages.

After some of these cross-infection experiments had been completed, it occurred to the writer that in nature a fly of one species must often ingest by fecal contamination of its food flagellates indigenous to other species. Perhaps some of these accidentally ingested organisms had originally come from the same species of fly as the one to which the infected material was fed. In such a case it might follow that the infection which appeared in the inoculated fly might actually have been caused by one or more parasites, which originally came from the same species of fly as the intentionally inoculated fly, and that the infection so produced did not come at all from the parasites indigenous to the other species. For example, a fly of the species *Musca domestica* might eat a drop of liquid garbage upon which a fly of the species *Phormia regina* had previously deposited its excreta contaminated with cyst and flagellated forms of Herpetomonas. If now the contents of the intestine of this *Musca domestica* were fed to a "clean" *Phormia regina,* it is quite certain that the Phormia would become infected whether or not the parasites supposedly indigenous to *Musca domestica* played any part in producing the infection.

It was decided to pass the Herpetomonas from one species of fly through a number of hosts of different species in order to eliminate this possibility of error. Accordingly, the following two experiments were carried out:

Experiment A. August 15. Herpetomonas from "wild" *Lucilia sericata* was fed to "clean" *Phormia regina.*

August 30. The intestinal contents of one of the heavily infected *Phormia regina* (inoculated August 15) was fed to "clean" *Sarcophaga bullata.*

September 7. The intestinal contents of one of the heavily infected *Sarcophaga bullata* (inoculated August 30) was fed to "clean" *Lucilia sericata.*

September 20. Examination showed that some of the *Lucilia sericata* (inoculated September 7) were infected.

Experiment B. September 24. *Herpetomonas* from "wild" *Lucilia sericata* was fed to "clean" *Sarcophaga bullata.*

October 7. Examination showed that some of the *Sarcophaga bullata* flies inoculated September 24 were infected with *Herpetomonas.* Ten which were not examined were placed in a jar containing a number of "clean" *Phormia regina flies.*

October 31. Six of the seven *Phormia regina* remaining alive were found to be infected with Herpetomonas. Three of the *Sarcophaga bullata* which remained alive were infected with Herpetomonas.

From ten to twenty of each lot of laboratory bred flies were examined as a precaution against accidental contamination and "hereditary" transmission through the ovary. No laboratory bred flies were ever found to be infected which had not been purposely inoculated *per os*.

The results of these experiments preclude the possibility that the infections were carried out with contaminated material. It is unthinkable that the parasites from Lucilia would passively be carried through Phormia and Sarcophaga, and twenty-three days after the time they were taken from Lucilia again be infective to it (Experiment A). The further likelihood that the first Lucilia carried in its intestine flagellates indigenous to Phormia and Sarcophaga is slight.

Experiment B justifies much the same conclusions as Experiment A, and in addition shows that herpetomonads which were taken from one species of fly and passed through two hosts of another species could infect a fourth species by fecal contamination, the probable natural method of transmission of the parasite. It might be added that these two experiments demonstrate the non-specificity of *H. muscae-domesticae* quite as well as the previously noted experiments, although not so many species of flies were used.

It was found that one species of fly might be infected with herpetomonads from other species by inoculation *per os* with the contents of the entire infected intestine diluted with saline solution. The question arises whether cross-infection of species occurs in nature or whether in nature certain peculiar biological conditions obtain which prevent this, as Roubaud (1912) has suggested. If a piece of putrifying meat is put outside the window on a warm summer day and watched, one can observe that many different kinds of flies alight upon the meat to feed or to deposit their eggs. I have observed Phormia and Lucilia in large numbers, Sarcophaga of various species, Calliphora, Cochliomyia, *Musca domestica, Muscina stabulans*, and other species of flies settle upon the same piece of meat in the course of one-half of an hour. Apparently, conditions are quite favorable for contamination of the food of a fly with excreta from flies of other species.

In order to determine whether or not natural cross-infection actually obtains, the following experiment was carried out:

Experiment C. About fifty "wild" Lucilia were captured and released in a glass aquarium jar in the bottom of which was a dead rat with intestines exposed. The flies were given an opportunity to contaminate the rat with their feces for a period of two hours. Fifteen of the flies were examined for Herpetomonas, nine of them being positive. These Lucilia flies were released, and a number of Phormia,

Lucilia and Sarcophaga flies were liberated within the aquarium jar. After they had fed upon the rat for six hours, the flies were etherized, placed in clean glass containers, and fed dilute sugar solution. Twelve days later the flies were examined for Herptomonas with the following results:

Species	Number Examined	Positive Infections
Lucilia sericata	18	10
Phormia regina	21	13
Sarcophaga bullata	10	2
Controls		
Lucilia sericata	10	0
Phormia regina	10	0
Sarcophaga bullata	10	0

It is evident from the above data that the infected Lucilia flies could transmit the infection to flies of the same and of two other species under conditions as nearly natural as is possible to make them in the laboratory.

DISCUSSION

Roubaud (1912) attempted to infect *Pycnosoma putorium* with "*Cercoplasma*" *mirabilis,* Leptomas from Pyrellia and *Cystotrypanosoma grayi* from Glossina. In the absence of positive results he drew the conclusion that the facts indicate a great degree of specificity of the different types of flagellates for their muscoid hosts. Likewise, the morphological studies of Chatton and Leger (1911) seem to indicate that each species of Drosophila has its own type of parasite. These results are hardly what one should expect, judging not only from the experiments with *Herpetomonas muscae-domesticae,* but also from the evidence furnished in the case of trypanosomes and their intermediate hosts. It has been demonstrated that *Trypanosoma lewisi* develops in almost every species of flea with which experiments have been carried out. Furthermore, it develops in the rat louse, *Haematopinus spinulosus,* and in the bed-bug, *Cimex lectularius* (Minchin and Thompson 1915). *Trypanosoma cruzi* develops in four species of the genus Triatoma and in one species of Rhodnius. It is not surprising that Herpetomonas, which is closely related to Trypanosoma biologically, should show a lack of rigid adaptation to a particular species or genus of host.

Alexeieff (1913) laid down the two following principles as a basis for general parasitology:

1. One species of parasite may be harbored by different hosts, sometimes quite removed from each other in the zoological scheme.

2. A host may harbor two or more closely related species of parasites.

There can be no disputing the correctness of these two fundamental concepts. The herpetomonads of at least six muscoid flies are easily transferable from one species of host to another. Then there is the evidence from the non-specificity of trypanosomes for their intermediate hosts. This and much more evidence might be brought to bear in support of the first principle. Probably as many facts could be marshaled for the second principle as for the first. The muscoid fly *Calliphora erythrocephala* is known to harbor two distinct types of Herpetomonas (Swellengrebel 1911). The rat flea may harbor both Herpetomonas and *T. lewisi* often to the confusion of the investigator. Anyone without practical experience who attempts to distinguish between the free-living stages of the human amoebae, *Endamoeba coli* and *Endamoeba histolytica* will realize the truth of this second principle of Alexeieff.

While it is important to realize the non-existence of absolute specificity of the parasites for their hosts, it must be kept in mind that some parasites do manifest a most rigid choice of host. The human plasmodias, trypanosomes of some of the lower animals, and among others, many of the intestinal protozoa of man, have never been successfully cultivated in any animal other than their indigenous hosts. But instances of this nature should not supply an *a priori* justification for neglecting to investigate the specific host relationship of animal parasites.

SUMMARY

1. The type of Herpetomonas known as *H. muscae-domesticae* was found to be entozoic in the alimentary canals of the muscoid flies *Musca domestica, Phormia regina, Lucilia sericata, Sarcophaga bullata, Cochliomyia macellaria* and *Calliphora erythrocephala.*

2. The flagellate from any one of these six species of "wild" naturally infected flies was capable of producing a natural infection in the other five species of "clean" laboratory bred flies when inoculated *per os* (Experiments 1 and 6).

3. That cross-infection was not due to accidental contamination was demonstrated by passing the parasites through a number of hosts of different species (Experiments A and B).

4. Such infected flies are "carriers" capable of infecting other flies by fecal contamination of the food or proboscis of the fly (Experiment B).

5. It is extremely probable that *Herpetomonas muscae-domesticae, H. luciliae, H. calliphorae, H. sarcophagae,* and the Herpetomonas from Phormia and Cochliomyia flies all represent the same species.

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NOTES ON SOME FURCOCERCOUS LARVAL TREMATODES *

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The larval trematode fauna of North America is only incompletely known. Previous to the work of Cort (1914) there were only scattered fragmentary records; after him Faust alone has contributed much in this field. The present writer has made an attempt to add to the knowledge of the morphology and relationships of one particular group, the furcocercous larvae; this investigation is timely in view of the renewed interest taken in the forked-tailed cercariae by virtue of their relation to schistosomiasis.

Sewell's recent monograph of the Indian forms (1922) is excellent, but his lack of personal acquaintance with only partly known, or incorrectly reported, North American larvae has introduced in his scheme of relationships certain errors which may now be corrected. In the present work a number of described forms have been restudied, and seven new species reported from two regions of the United States; several of the latter peculiarly fit into the existing knowledge of the furcocercous larvae and enable some definite groups to be formed. These new data, with a review of the literature, make it possible to present a consideration of all known forms and to submit a scheme of relationships. The present study was begun in 1920 and has been carried out under the direction of Professor Henry B. Ward, to whom the writer is indebted in many ways; he also wishes to acknowledge the courtesies extended by Dr. G. R. LaRue during the summer of 1921 at the University of Michigan Biological Station.

In the matter of nomenclature the lead of Sewell has been followed in the use of "salivary gland" for the large cells, usually four or more in number, which occupy a considerable part of the body and empty through thick ducts opening on the extreme anterior end. "Head gland" has been used to designate the "Kopfdrüse" of Narabayashi (Cort, 1919: 498), rather than the confusing term "oral" gland of Khalil (1922); Sewell has also been followed in the use of "anterior organ" in place of "oral sucker." In the description of the excretory systems the nomenclature has been compiled from that used by Cort, Faust, Sewell, and Soparkar.

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* Contributions from the Zoological Laboratory of the University of Illinois, under the direction of Henry B. Ward, No. 225.

NEW MONOSTOME CERCARIAE STUDIED

Cercaria multicellulata spec. nov.

This small monostome larva was found in the digestive gland of *Physa gyrina* Say from the vicinity of Urbana, Illinois, on two occasions in the fall of 1922. It is the third longifurcal monostome to be reported, the first being *C. rhabdoceca* Faust 1919 and the second *C. indicae XXVII* Sewell 1922.

The details of internal structure are made out with very great difficulty, as the entire body is packed with small parenchyme cells; the most conspicuous structures are the eye-spots, composed of a varying number of irregularly-shaped pigment granules. The sides of the body are generally parallel, with a decided tapering in the region of the anterior organ; in contraction under a cover-glass the body is frequently crenated (Fig. 5). Measurements taken under various conditions show the maximum body extension under a cover-glass to be 184μ; the average of specimens squirted into hot Gilson's fluid is 165μ by 28μ for the body, tail-stem 198μ, furcae 147μ; and of those mounted in Canada balsam, the body is 136μ by 26μ, tail-stem 196μ by 24μ, furcae 147μ.

The anterior organ varies in form from that of a prolate spheroid to a more pyriform and even to a dumbbell shape. Rather coarse retrorse spines cover the anterior end and apparently diminish in size and number posteriorly. No trace of a ventral sucker could be found.

The tail-stem is cylindrical, of somewhat less diameter than the body, and contains a varying number of large gland cells. The surface is annulated, and furnished with a number of fine sensory hairs which can only be seen under the most favorable conditions. Cross-sections of the tail-stem reveal four principal muscle fields. In the living animal the furcae are about equal in length to the tail-stem, and are not constricted off from it. There are small spines distributed over its surface, and a narrow delicate paddle edge around the distal half. No trace of an alimentary canal can be found; the three pairs of salivary gland cells stain deeply with intra-vitam neutral red, and are acidophilic to eosin in sections. Closely associated with the openings of the ducts are about a dozen piercing spines.

Eight pairs of flame cells are found in the body and two pairs in the tail-stem (Fig. 5). While the exact connections of the capillary connecting tubules could not be made out, their locations in pairs makes it possible that they have the same pattern as that of *C. rhabdoceca* Faust. A small island of Cort is probably present; the caudal excretory tube bifurcates distally and each branch opens in the mid-furcal region.

Two rather definite cell masses represent the reproductive system of the adult, a large group posterior to the salivary gland cells and anterior to the bladder, and a smaller mass between the first two pairs of salivary

glands. The parthenitae are very elongate sporocysts of narrow calibre, the cercariae developing in batches between irregularly-placed constrictions; a birth-pore is present near the anterior end of the sporocyst.

Cercaria hamata spec. nov.

In the fall of 1922 another small monostome larva with long furcae was found on three occasions in *Planorbis trivolvis* from Urbana, Ill. It is superficially much like *C. rhabdoceca* Faust, but has important differences; the lack of simple eye-spots easily distinguishes it from *C. multicellulata.*

The body is almost constantly a long cylinder (Fig. 2), except when annulated during extreme extension. The diameter of the posterior part is practically equal to that of the tail-stem, and the shape of the body shown by Faust (1919: 330) for *C. rhabdoceca* was never observed. When sinking motionless through the water the anterior part of the body is bent upon the ventral surface so that the body is hook-shaped. The body of mounted specimens averages 179μ by 28μ, tail-stem 248μ, furcae 198μ; while for the living larvae, motionless under a cover-glass exerting practically no pressure, the body measures 207μ by 41μ, tail-stem 276μ, furcae 276μ.

The spination is the same as that represented for *C. multicellulata.* No trace of a ventral sucker could be found. The tail-stem is very similar to that of *C. multicellulata* in the character of the wall and the sensory hairs, although the number and size of the caudal glands are such that the entire lumen is filled with them. What Sewell (1922: 61) has described as "short lateral branches" (excretory) are probably the spaces between caudal gland cells. Cross-sections of the tail-stem show four rather prominent muscle fields. Distal thin edges are not present on the furcae. A short rhabdocoel gut, with a pharynx, is present (Fig. 2), although seen with difficulty. The same number and kind of salivary glands are present in *C. hamata* as were found in *C. multicellulata,* although the distribution with relation to the small anterior germ cell mass is frequently irregular. The staining reactions of the coarsely granular protoplasm are the same in both species. The ducts of *C. hamata* are almost contiguous throughout the greater part of their length; solid piercing spines are present on the anterior tip.

The number and relations of the flame cells in the two species appear to be identical, so that with the exception of the bladder shape the figure for *C. multicellulata* may be taken to represent the excretory system of *C. hamata.* As noted above, the great number of small parenchyme cells makes the determination of the exact arrangement of the capillaries a matter of extreme difficulty; it is probable that both species have tufts of vibratile cilia in the main lateral collecting tubes. The relative sizes and positions of the two germ cell masses are essentially the same

in *C. multicellulata* and *C. hamata*. The parthenitae do not differ markedly; both contain orange and yellow pigment granules in the walls.

NEW DISTOME CERCARIAE STUDIED

Cercaria elvae spec. nov.

Two specimens of *Lymnaea stagnalis* var. *appressa* from the Douglas Lake region of Michigan were found in the summer of 1921 to harbor a new distome larva; its nearest known relatives are *C. ocellata* Ssinitzin and *C. bombayensis no. 19* Soparkar. The general behavior of the larva while freely swimming and during locomotion on a substratum, either with or without a cover-glass, is very similar to that described by Cort for the cercaria of *Schistosoma japonicum*, although the two species are quite different in certain respects.

The body of living, emerged individuals averages 368μ by 80μ, tail-stem 501μ, furcae 328μ, while well extended specimens in balsam mounts measure 368μ by 41μ for the body, tail-stem 382μ, furcae 290μ. The large body tapers both anteriorly and posteriorly from the ventral sucker, which is located in the posterior third; the deeply pigmented "compound" eye-spots stand out in sharp contrast to the hyaline body of the living animal. Because of the protrusion of the ventral sucker the cercaria is usually seen, under a cover-glass, lying on its side; powerful muscles run dorsally to the body wall (Fig. 3). The body, tail-stem, and furcae are finely and evenly spined. The tail-stem is a powerful organ, attached terminally and showing in cross-section four principal and two subsidiary muscle fields, the former composed of numerous fibers. The anterior organ occupies a third of the body and is divided into a thin- and a thick-walled portion, the latter being the smaller posterior end. A conspicuous head gland, containing coarsely granular protoplasm which is eosinophilic in mounted sections, occupies the anterior thin-walled part.

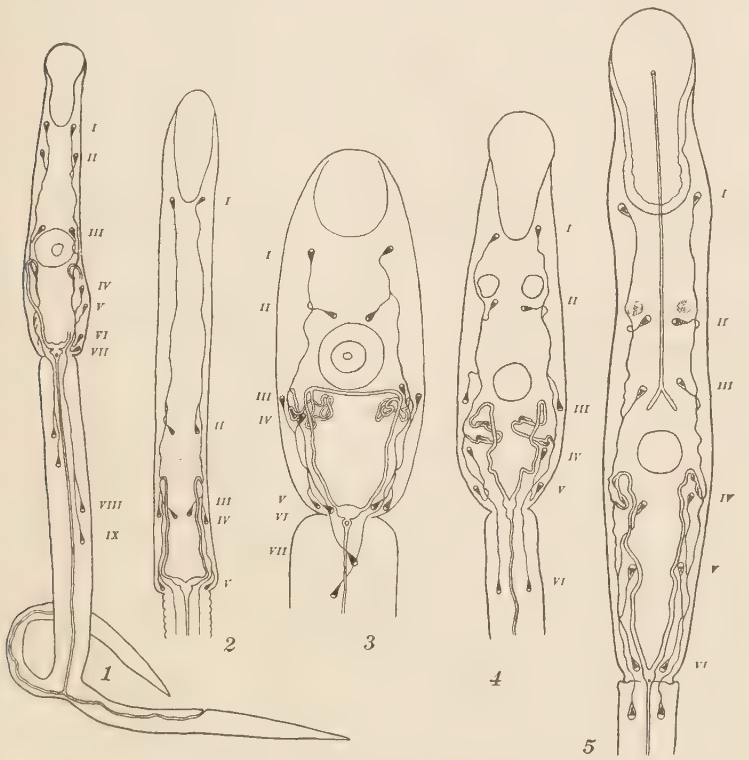
The alimentary canal opens ventrally behind the anterior tip, continues as a very fine tube through the anterior organ, and bifurcates into short ceca just anterior to the ventral sucker. No trace of a pharynx is present. The nervous system is represented by a large H-shaped mass anterior to the eye-spots. The most prominent structures of *C. elvae* are the anterior set of four and the posterior group of six salivary gland cells, the former being coarsely granular and weakly eosinophilic, and the latter finely granular and, in mounted sections, basophilic to hematoxylin.

The pattern of the excretory system has been worked out in detail (Text-fig. 5); except for minor details it is identical with that of *C. bombayensis no. 19* Soparkar. The single large mass representing

the reproductive system is posterior to the ventral sucker. The parthenitae are unknown, as the snails died and disintegrated during the absence of the writer.

Cercaria wardi spec. nov.

A large larva possessing a peculiar mucin gland was found in the digestive gland of *Planorbis trivolvis* from the Urbana region in 1921; this cercaria has a striking body form (Fig. 11). It is somewhat smaller



Ventral views of excretory systems of five furcocercous cercariae.

1. *Cercaria chrysenterica*
2. *Cercaria tenuis*
3. *Cercaria burti*
4. *Cercaria wardi*
5. *Cercaria elvae*

than its nearest known relatives, *C. bombayensis no. 13* Soparkar and *C. indicae XXV* Sewell; in well-extended individuals freshly mounted in balsam the body measures 265μ, tail-stem 682μ, furcae 237μ; maximum sizes of the living animal are: body 467μ, tail-stem 730μ, and tail-stem including furcae 935μ.

The anterior organ is not so conspicuously divided into regions as in *C. elvae;* a head gland is present. The powerful ventral sucker

protrudes so prominently that it is difficult to secure a frontal view of the active larva. The tail-stem is more than twice as long as the body, to which it is attached somewhat ventrally; four principal muscle fields are seen in cross-sections of the former. The furcae have fluted paddle edges.

The type of alimentary canal is that found in *C. elvae,* except that the ceca are relatively larger; there is no trace of a pharynx. Just posterior to the large H-shaped mass of the nervous system is a pair of large cup-shaped eye-spots formed by coarse brown-black pigment granules. Two sets of salivary glands are present, four anterior-dorsal coarsely granular cells and a posterior-ventral group of six cells with finely granular protoplasm; the former are acidophilic to eosin and the latter basophilic to Delafield's hematoxylin. A large irregularly-outlined gland is present in the posterior end of the body, extending laterally on either side to the region of the eye-spots; its contents are probably of a mucin nature and it has been designated as the "posterior mucin gland."

The details of the excretory system (Text-fig. 4) are essentially identical with those of *C. bombayensis no 13;* the branches in the furcae open at the tips. A single large mass of germ cells is found between the salivary gland cells and the posterior mucin gland. The cercariae develop in elongate, irregularly-constricted sporocysts.

Cercaria burti spec. nov.

A furcocercous larva possessing a cross-commissure of the bladder similar to that of *C. douglasi* Cort 1917 was found in the same region of Michigan in the summer of 1921.

Under a cover-glass the living body is considerably contracted to a decided oval shape and the animal is generally rather sluggish; the short blunt-ended cylindrical form (Fig. 8) is characteristic of permanent balsam mounts. The maximum body length of living larvae is 240μ, while contracted ones measure 125μ; the average of a number of well-extended individuals in fresh balsam mounts gives 134μ by 35μ for the body, tail-stem 140μ by 26μ, furcae 157μ.

The anterior organ is a short prolate spheroid, without divisions into thin- and thick-walled parts; no trace of a head gland is present. The ventral sucker is a powerful organ of attachment, rarely protruding much from the ventral surface; a dorso-ventral view of the body is the one usually obtained. The tail-stem is attached posteriorly; the caudal glands, usually visible only in living animals, may be seen in well-preserved, mounted specimens. The mouth opening is terminal, being followed by a prepharynx, pharynx, esophagus, and rather slender ceca which terminate only a short distance posterior to the ventral sucker in two disjoined parts. An H-shaped nervous system is present;

no eye-spots are found. Four pairs of salivary gland cells are located in the dorsal posterior part of the body, between the ventral sucker and the main mass of germ cells.

Although the total number of flame cells in *C. douglasi* and *C. burti* is the same, the distributions differ with respect to the point where the anterior and posterior collecting tubules pour into the bladder arms; in *C. douglasi* there are three cells anterior and two posterior on either side of the body, and two cells in the proximal tail-stem region where only one is present in *C. burti* (Text-fig. 3). The excretory openings are mid-furcal. The parthenitae are long, thin-walled sporocysts containing great numbers of cercariae at irregular intervals; a subterminal birth-pore is present (Fig. 6).

Cercaria tenuis spec. nov.

Two specimens of *Planorbis trivolvis* collected in 1921 from a swamp near Burt Lake, Michigan, were parasitized with a very slender-bodied, longifurcal, pharyngeal larva; it is chiefly interesting in that the form which it most resembles is *C. indicae XXII*, an Indian representative of the very small group of longifurcal forms which do not possess pharynges. The body form of *C. tenuis* (Fig. 4) does not undergo the striking changes in shape observed in *C. burti* and *C. chrysenterica* although it is capable of considerable change in length. Apparently the spination is limited to the anterior cap. For the living larva the maximum size of the body is 288μ, tail-stem 204μ, furcae 240μ, while in well-extended individuals mounted in balsam the body measures 225μ by 21μ, tail-stem 215μ by 21μ, furcae 207μ.

The anterior organ is frequently pyriform; there is no sharp division into anterior and posterior regions. No structure homologous to a head gland appears to be present. The ventral sucker is about one-quarter of the body length from the posterior end, measuring about 25μ in diameter in living specimens. There is but a single row of hooked spines, twenty-two in number, around the margin; the hooks are on the periphery and point in toward the center. The tail-stem has the finely annulated appearance seen in many longifurcal larvae; about five pairs of irregularly-arranged caudal glands are present.

The mouth opening is subterminal; there is a pharynx, about 9μ in diameter, and the narrow ceca extend to the posterior edge of the ventral sucker, each contiguous with two disjoined parts. No eye-spots are present. Four small salivary gland cells are found between the bifurcation of the esophagus and the ventral sucker; the protoplasm is coarsely granular, and is eosinophilic in mounted sections. There are apparently about eight solid piercing spines dorsal to the gland duct openings. Five pairs of flame cells are distributed through the body and two pairs are found in the tail-stem (Text-fig. 2). The excretory

openings are mid-furcal. A considerable mass of germ cells is located just posterior to the ceca. The parthenitae are elongate sporocysts which have a subterminal birth-pore.

Cercaria chrysenterica spec. nov.

A new longifurcal larva was found in one specimen of *Lymnaea megasoma* from the Burt Lake region of Michigan; its nearest known relative is probably *C. emarginatae* Cort. The form changes of the body in active motion under a cover-glass are numerous; a club shape is commonly assumed (Fig. 1). The average sizes of well-extended specimens mounted in balsam are 260μ by 48μ for the body, tail-stem 244μ, furcae 248μ; the maximum body length of a freely moving individual under a coverglass is 384μ. The anterior organ is pyriform, with the small end directed inward; a head gland is lacking. The ventral sucker is a relatively large structure, located about two-thirds of the body length from the anterior end. Behind an oral cap of retrorse spines there are indications of bands of small spines on the body surface back to about the ventral sucker region. The tail-stem is attached posteriorly to the body; its surface is finely annulated and it contains on the average six pairs of caudal glands.

The mouth opening is subterminal; a pharynx is present around the narrow esophagus, which bifurcates in the mid-body region into two large club-shaped ceca. In the living animal these are golden yellow in color, while in section the jelly-like contents are strongly eosinophilic. Four coarsely granular salivary glands are located ventrally in the body between the posterior germ cell mass and the ventral sucker; in section they are strongly eosinophilic. Seven pairs of flame cells are present in the body and two pairs in the tail-stem (Text-fig. 1); branches of the caudal excretory tube open in the mid-furcal region. The entire excretory pattern is quite different from that of *C. emarginatae,* which has five pairs of flame cells in the body, disposed in each lateral half into an anterior group of three and a posterior of two cells. The parthenitae are long sporocysts which vary somewhat in diameter throughout their length but do not have the very decided constrictions found in some species. A birth-pore is present near the anterior end.

DISCUSSION

The classification of the furcocercous larval trematodes presents many difficulties, due in part to the almost entire lack of knowledge of the life histories, and in a greater measure to incomplete descriptions and to the relatively undeveloped state of the organ systems, notably the reproductive. Furthermore, the older accounts have been based largely upon preserved materials, and therefore patterns of excretory systems, observable only in compressed living specimens, are very fre-

quently unknown; in view of the importance attached by recent students to the number and arrangement of the flame cells as indicative of relationships, it is difficult to critically consider a form for which these data have not been determined. The number and character of the salivary gland cells are also used, although the apparent diversity of this equipment in the three known human schistosome larvae, in contrast to the probable identity in excretory system pattern, discounts the value of these structures in the determination of relationships.

Sewell (1922: 247) has recently modified Cort's classification (1917) so as to form three groups of distome larvae, the members of the *first* being most readily distinguishable by the fact that the furcae are less than one-half the tail-stem length,* those of the *second* by the adequal length of these structures, and those of the *third* by a very distinct type of excretory system. The monostome furcocercous cercariae are separately considered.

The brevifurcal larvae (Group 1 of Sewell) have been the most carefully described, due to the attention devoted to them in the study of the causative agents of schistosomiasis, which are now known to be included in this group. Although two of the new species described in this paper fall into the monostome group, and three are longifurcal distomes, a scheme of classification is presented only for the better known brevifurcal distome larvae, together with a key for the separation of the groups.

BREVIFURCAL DISTOME CERCARIAE (GROUP I OF SEWELL)

APHARYNGEAL

Series I

Group A (Japonicum)

Cercaria of *Schistosoma japonicum*, described by Miyairi and Suzuki, 1913 (according to Cort, 1919)

Cercaria of *Schistosoma hematobium*, described by Leiper, 1915 (according to Faust, 1920; Bettencourt and da Silva, 1922)

Cercaria of *Schistosoma mansoni*, described by Leiper, 1915 (according to Faust, 1920; Khalil, 1922)

Cercariae indicae XXX Sewell 1922

In view of Khalil's recent work on the larva of Sch. mansoni it is probable that every member has three pairs of flame cells in the body and one pair in the tail-stem.

Group B (Spindalis)

Cercaria of *Schistosoma spindalis* Soparkar 1921

Cercaria "B" Kemp 1921

Cercariae indicae XLVII Sewell 1922

Cercaria "B" is included on the basis of the number of salivary glands and the general characters; the excretory system is unknown. Several other incompletely known forms, possibly belonging to either of the above two groups, are included here.

Cercaria blanchardi da Silva 1911

Cercaria "Leiper Fig. 46" Leiper 1915

Cercaria "Bahr and Fairley Fig. 5" Bahr and Fairley 1920.

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* Except Group D (infra).

Group C (Douthitti)

Cercaria douthitti Cort 1914

Cercaria "C" Kemp 1921

Although the last named larva is known only from preserved material, it is probably very closely related to *C. douthitti*, which has five pairs of flame cells in the body.

Series II

Group D (Elvae)

Cercaria ocellata Ssinitzin 1909

Cercaria bombayensis no. 19 Soparkar 1921

Cercaria elvae spec. nov. (described in this paper)

While the furcae of these larvae are greater than one-half the tail-stem length, other important characters place them close to the schistosome cercariae.

Series III

Group E (Bombayensis no. 13)

Cercaria bombayensis no. 13 Soparkar 1921

Cercariae indicae XXV Sewell 1922

Cercaria wardi spec. nov. (described in this paper)

All these forms possess the peculiar posterior mucin gland.

Group F (Wynaad)

Cercariae Indicae XXXVI Sewell 1922

Group G (Elephantis)

Cercaria echinocauda O'Roke 1917

Cercaria elephantis Cort 1917

The last-named species has five pairs of flame cells in the body; both have two sets of salivary gland cells. three pairs of small anterior glands and two pairs of larger posterior cells.

Group H (Gigas)

Cercaria gigas Faust 1918

The peculiar type of excretory system has been described by Faust; the larva possesses an anterior set of five pairs of gland cells and a posterior group of two pairs.

The exact relations of *C. "bilharziella"* Leiper 1915, *C. ocellifera* Lutz 1919, *C. oculata* Cawston 1917, and *C. parvoculata* Cawston 1919 cannot be determined until complete descriptions are available.

PHARYNGEAL

Series IV

Group AA

Cercaria "G" Yoshida 1917

Cercaria "F" Kobayashi 1919

Cercaria octadena Faust 1921

Until more complete accounts are published little can be said concerning their relationships; the first two are said to develop in rediae.

SUMMARY OF CHARACTERS

Series I, Groups A, B, C

Short furcae, less than one-half the tail-stem length; no furcal fin-folds. Body and tail-stem not greatly different in length. Alimentary canal rhabdocoel, or slightly modified from rhabdocoel. Eye-spots may be present.

Series II, Group D

Furcae somewhat longer than one-half the tail-stem length; furcal fin-folds in one larva. Tail-stem only slightly longer than body. Alimentary canal with short ceca. Eye-spots invariably present.

Series III, Groups E, F, G, H

Short furcae, less than one-half the tail-stem length; furcal fin-folds present. Tail-stem frequently very long. Alimentary canal with short ceca (except *C. Indicae XXXVI*). Eye-spots invariably present.

Series IV, Group AA

Pharynx present. Short furcae, less than one-half the tail-stem length.

Key for the Separation of Groups

1 (14) Pharynx absent...2
2 (13) Furcae less than one-half tail-stem length.....................3
3 (7) No furcal fin-folds; body and tail-stem not greatly different in length; eye-spots present or absent.........................4
4 (5, 6) Three pairs of flame cells in body.....................Group A
5 (4, 6) Four pairs of flame cells in body......................Group B
6 (4, 5) Five pairs of flame cells in body......................Group C
7 (3) Furcal fin-folds present; eye-spots present; tail-stem frequently very long...8
8 (9) With posterior mucin gland...............................Group E
9 (8) Without posterior mucin gland.................................10
10 (11, 12) Four pairs flame cells in body......................Group F
11 (10, 12) Five pairs flame cells in body......................Group G
12 (10, 11) Ten pairs flame cells in body.......................Group H
13 (2) Furcae somewhat longer than one-half tail-stem length....Group D
14 (1) Pharynx present......................................Group AA

Complete description of the new species reported in this paper will appear in a later publication.

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Explanation of Plate IV

Fig. 1.—*Cercaria chrysenterica;* ventral view of body and half of tail-stem, showing alimentary, salivary gland, and genital systems; caudal glands in tail-stem. $\times$ 350.

Fig. 2.—Semi-diagrammatic ventral view of body of *Cercaria hamata* showing alimentary, genital, and salivary gland systems. $\times$ 350.

Fig. 3.—*Cercaria elvae;* lateral view of body; salivary glands in two sets; head gland, eye-spots, nervous system, and portions of alimentary canal shown. $\times$ 365.

Fig. 4.—*Cercaria tenuis,* ventral view of body showing alimentary, nervous genital, and salivary gland systems. $\times$ 365.

Fig. 5.—Ventral view of body and part of tail-stem of *Cercaria multicellulata;* flame cells, genital and salivary gland systems, and caudal glands. $\times$ 675.

Fig. 6.—Anterior end of sporocyst of *Cercaria burti* showing birth-pore. $\times$ 70.

Fig. 7.—*Cercaria burti;* transverse section through ventral sucker region; intestinal ceca, salivary gland ducts, and germ cells shown. $\times$ 515.

Fig. 8.—Ventral view of entire *Cercaria burti;* caudal glands, mid-furcal openings of excretory system. $\times$ 220.

Fig. 9.—*Cercaria elvae;* transverse section through posterior part of anterior organ; salivary gland ducts, head gland, and capillary alimentary canal shown. $\times$ 500.

Fig. 10.—*Cercaria tenuis;* transverse section through tail-stem showing four muscle fields, and minute caudal excretory tube (central). $\times$ 765.

Fig. 11.—Lateral view of body of *Cercaria wardi;* alimentary, salivary gland, and genital systems; head gland and posterior mucin gland. $\times$ 300.

Fig. 12.—*Cercaria wardi;* outline showing lateral extension of posterior mucin gland. $\times$ 95.

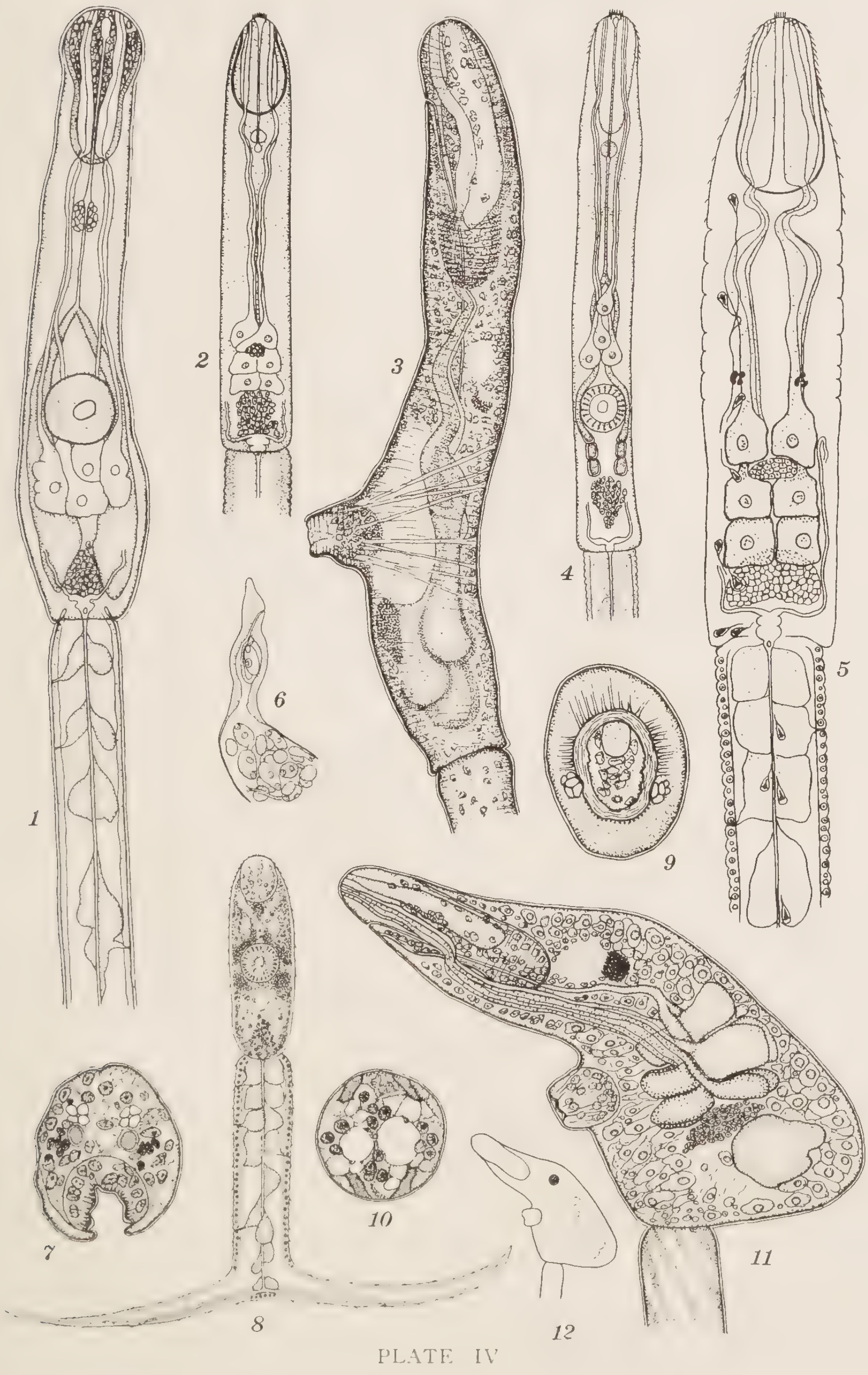

PLATE IV

OBSERVATIONS ON THE CYSTS OF *ENDAMOEBA COBAYAE* *

Francis O. Holmes

Although the trophic form of the guinea pig amoeba, *Endamoeba cobayae*, is fairly well known, its cysts have received only the slightest mention in the literature on account of their rare occurrence in the feces. Chatton mentioned them briefly in 1917. Because he was interested at the time in pointing out the differences between this species and *Endamoeba histolytica* he called attention to the resemblance of *E. cobayae* to *E. coli*, especially noting their eight-nucleate cysts.

During the next year Leger reported cysts in guinea pigs in French Guiana. He did not know whether these belonged to the species *E. histolytica* or to a new form, but from his account it is quite possible that they were immature cysts of *E. cobayae*. They were 14μ in diameter, had no more than four nuclei, and showed at times the histolytica type of chromatoids. The chromatoids of *E. histolytica* are rounded rods, few in number, always smooth in contour; those of *E. coli* are often more numerous, splintered or thread-like, typically of irregular outline. These two types will be referred to as the histolytica and coli types of chromatoids.

The object of this note is to present a brief description of the cysts, together with a few characteristic pictures, showing the appearance of the nuclei, chromatoids, glycogen vacuole, etc. It was noted recently that certain slides made from guinea pig cecal contents showed a few slightly abnormal cysts. Search was therefore made to discover whether the contents of the large intestine also contained cysts, or whether these disappeared before reaching the lower part of the intestine, as seemed probable from their rare occurrence in the feces.

When present in the cecum the cysts persisted and could be seen in ordinary fecal smears. In some cases the feces from the guinea pig cages also showed fair numbers of cysts. One guinea pig in particular seemed to be heavily infected. It was isolated and examined immediately after death, which occurred a few days later by reason of an experimental trypanosome infection. But in the meantime the guinea pig had become negative for cysts. Not only had they disappeared from the feces, the contents of the large intestine and the cecal material, but the trophic forms had decreased in number or had altogether died out so that they could not be found in the cecum at all. It is evident from this

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case and from others seen in the laboratory that cysts appear only occasionally; and that infections may persist in individuals for relatively brief periods and then disappear.

DESCRIPTION OF CYST

The average diameter of the cyst of *Endamoeba cobayae* is 14μ; most individual measurements lie between 12μ and 16μ; though some are as small as 11μ and others as large as 17μ, as may be seen from the following list of twenty individual measurements, recorded in microns:

16, 13½, 11½, 16, 14, 14½, 11, 13, 13, 13, 15, 12, 14½, 13, 13, 16, 14½, 16, 14, 17.

Mononucleate cysts have not been observed. Binucleate forms show one large glycogen vacuole, which presses the nuclei close to the wall (Fig. 1). Numerous small rod-shaped chromatoids are seen occasionally at this stage. Adult cysts, which have eight nuclei, are common (Fig. 2) but often slightly abnormal in that the cytoplasm is shrunken from the wall (Fig. 4.) Yet the latter is still perfectly spherical and entirely capable of resisting vital stains used to indicate dead or dying individuals. Neutral red in a 1:1000 aqueous solution was the stain actually used, and its inability to penetrate the cysts together with the normal appearance of the nuclei in hematoxylin stains seem sufficient evidence that the shrunken specimens are still alive and probably capable of developing under favorable conditions. Occasionally remnants of chromatoids are seen. They are few (1 to 4) in each cyst, do not stain very sharply and have the appearance of having been partly dissolved so that their smooth contour is not an indication of a strict resemblance to *Endamoeba histolytica* chromatoids.

The eight nuclei of the mature cysts show all the typical appearances seen in similar cysts of *Endamoeba coli*. The peripheral chromatin varies from an even layer on the nuclear membrane to a few large blebs distant from each other, connected by the thin nuclear membrane free from chromatin. The karyosome may be dispersed in several dots, partially aggregated into a kidney-shaped body, or fully aggregated into a single dot (Fig. 4). When the karyosome is dispersed and consists of several small dots it lies near the center of the nucleus; as it aggregates it leaves this position and approaches the wall till it reaches a position about half way from the center of the nucleus to the periphery in its final characteristic dot stage. On the whole it is less eccentric here than in the typical nucleus of the motile form.

BIOLOGICAL CHARACTERS OF THE AMOEBAE

In an attempt to discover the stimulus prompting encystment sections of the cecum and cecal contents were made. It was thought that

perhaps the tropic amoebae would be found aggregated close to the wall of the cecum: it would then have appeared likely that encystment followed the change in environment when individuals were washed from the wall and surrounded by the intestinal contents. Actually the amoebae were found rather evenly distributed throughout the contents, by no means massed on the walls. No greater concentration was observed there than at any point in the interior. At a distance from the wall some of the amoebae were found to have penetrated large, partially digested plant cells, and to have divided there, surrounded by bacteria which had already crowded the space by their own repeated divisions. These were typical feeding amoebae, normal in the appearance of their food vacuoles, and evidently capable of dividing.

It may be concluded that encystment is not stimulated by the sudden removal from the environment of the intestinal wall to that of the

EXPLANATION OF FIGURES

Camera lucida drawings from specimens fixed with Schaudinn's fluid and stained with iron hematoxylin. × 1500.

(1) Binucleate cyst with one large glycogen vacuole pressing the cytoplasm, with its nuclei and small chromatoids, close to the wall. (2) Normal eight-nucleate adult cyst, showing two chromatoid remnants. (3) Parasitized cyst; bacterial colony from one vacuole has broken out into the general cytoplasm and has separated into pairs of cocci. (4) Adult cyst, with cytoplasm slightly shrunken; nuclei show various states of aggregation of the karyosome. Such shrunken cysts do not appear to be dead, as is pointed out in the text. Note that drying would have caused a different type of shrinkage in which the cyst wall would have been involved.

contents, as might be the case in such tissue feeders as *Endamoeba histolytica,* but by some other factor, as yet unknown, operating without involving a marked change in the position of the amoeba.

Recently a slightly unusual amoeba was found in a laboratory white rat. It differed from *Endamoeba muris* notably in the presence of nearly typical histolytica chromatoids, few in number and smoothly rod-shaped. The appearance of the numerous small chromatoids noted in the immature *Endamoeba cobayae* cysts indicated the possibility that the rat infection might be from this species, although such transfers had not been noted before, and though the cysts in the rat were not at all abnormal and were very numerous. Apparently they were more normal to the white rat than *Endamoeba cobayae* is to the

guinea pig. Infection experiments were immediately tried. Two white rats were fed repeatedly with guinea pig amoeba cysts, and allowed to associate for some time with guinea pigs which passed cysts in their feces. Their drinking water also contained cysts. Two others had trophic forms of the amoeba injected directly into their caeca. No cysts were found in their feces following this treatment, and subsequently no amoebae were found in their ceca.

It may be concluded then that *Endamoeba cobayae* is not easily transferred to the white rat and that the amoeba of the white rat probably is not identical with the species under discussion.

PARASITES IN THE AMOEBAE

In a binucleate cyst a colony of some parasite seemed to be thriving. More often the trophic amoebae show such colonies. From their size and general appearance it seems likely that these bodies are bacterial in nature, perhaps arising from individuals ingested as food, but capable of resisting the fluids of the food vacuole and of dividing and growing within the body of the amoeba. The size and shape of the cells vary considerably. In one nearly mature cyst, in which the parasites have broken out of their vacuole, they are seen to be cocci grouped in pairs (Fig. 3).

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A NEW CETACEAN CESTODE*

(*Prosthecocotyle monticellii* sp. nov.)

With a Note on the Genus Tetrabothrius Rudolphi

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Medical Department, University of Georgia

A Blackfish (*Globicephalus melas*), 450 centimeters in length, was found dead on the beach of Vineyard Sound, near Falmouth, Mass., July 3, 1920. It was brought to the laboratory of the Bureau of Fisheries, Woods Hole, Mass., on July 5. The stomach contained many jaws and lenses of squid, and one squid jaw was found in the intestine. The specimen was a female, recently delivered (MacCallum, 1920). The intestine measured 4312.5 centimeters in length, and was of nearly uniform diameter throughout, the duodenal portion only being slightly enlarged; chyle, in all but the posterior fourth deeply stained green with bile.

Entozoa found were two nematodes in the stomach, one of them 76 mm. in length, with the head macerated, the other a small Ascaris, slightly macerated; about sixteen specimens of an Echinorhynchus, and the cestodes, which are described in this paper. They are of interest primarily on account of the very few cestodes in the adult stage which have been described from cetaceans.

Recent writers on avian cestodes have referred Monticelli's genus Prosthecocotyle to the genus Tetrabothrius Rudolphi. Thus Ransom (1909; 59) gives as synonyms of Tetrabothrius Rudolphi: Amphoterocotyle Diesing 1863 (type *A. elegans* Dies. 1863), Prosthecocotyle Monticelli 1892 (type *Taenia forsteri* Krefft 1871), Bothridiotaenia Lönnberg 1896 (type *Taenia erostis* Lönnberg 1889). This is no doubt a correct disposition of Diesing's and Lönnberg's genera. It is to be noted, however, that, while Diesing and Lönnberg were dealing with cestodes of birds, Monticelli was considering a cestode from the cetacean *Delphinus delphis*. It is hardly to be expected that closely related cestodes should be found in such widely dissimilar hosts as birds and cetaceans. However that may be, a comparison of this cestode from the blackfish with figures and descriptions of such typical avian cestodes as *Tetrabothrius macrocephalus* (Rud.) and *T. erostris* (Krefft), and with examples of this genus which I have collected from

* A part of the laboratory work upon which this paper is based was done at the laboratory of the Bureau of Fisheries, Woods Hole, Mass., and of the Zoological Department of the University of Missouri.

birds, shows no such resemblance as a generic kinship demands. On the other hand its resemblance to *Prosthecocotyle forsteri* (Krefft) seems to be sufficient to justify referring it to the same genus. If this conclusion is correct, then the names used by Monticelli should stand. They are: *Prosthecocotyle forsteri* (Krefft) from *Delphinus delphis,* and *P. triangulare* (Dies.) from *Delphinorhynchus rostratus.*

To this list is to be added the cestode from the blackfish for which I propose the specific name, *monticellii,* in honor of the distinguished author of the generic name Prosthecocotyle.

Prosthecocotyle monticellii sp. nov.

The four bothria are arranged in dorso-ventral pairs; each is provided with a relatively large muscular sucker, and with three small auricular appendages, which are continuous with the muscular border of the sucker. One appendage is at the anterior end, and on the front face of the bothrium, the others are at the posterior angles, and on the under side.

There is an unsegmented portion back of the scolex; first segments very short, later increasing somewhat in length, posterior edge of proglottides projecting slightly, thus making a finely serrate margin on the strobile. Genital pores on one margin of the strobile, at about the middle of the length of a proglottis, provided with a muscular atrium, into which both vagina and cirrus open. The cirrus is small and unarmed. The cirrus-pouch is small and encloses a few coils of the vas deferens (Fig. 5). The vas deferens is voluminous, its coils lying along the anterior border of the proglottis for a distance equal to about one-third the breadth of the proglottis. The testes are in the anterior portion of the proglottis in front of the ovary. Their exact number was not determined. There appear to be from twelve to fifteen in sections of proglottides, although not so many as that could be made out in whole mounts. The vagina lies along the ventral side of the cirrus-pouch and opens beside the cirrus in the genital cloaca. It follows a more or less tortuous course and ends in a relatively large seminal receptacle at the median line. The ovary is relatively large and fills the greater part of the posterior half of the proglottis. The vitelline gland is small, and lies in front of the ovary on the median line.

There is considerable variation in shape and size in the cells of the ovary. The larger cells are oval-elliptical, with large nuclei, and measure about 24 by 12μ. Cells measuring from 3 to 21μ were found in the same section. Most of the cells in this case were circular in outline, some were oval-elliptical. One large, wedge-shaped cell was noted which measured 42 by 30μ in the two principal diameters. The longitudinal muscles are rather fine, and, in most of my sections exhibit but little tendency to become fascicled, and showing in but a few

sections a hint of the arrangement into two layers of fascicles which is characteristic of the genus Tetrabothrius of birds. The layer of circular muscles which surrounds the parenchymatous area is rather strongly developed.

Sections of mature portions of the strobile show a very thin body wall, in some cases measuring only 0.03 mm. in thickness. The longitudinal fibers are here very minute, while the circular fibers are still relatively strongly developed. The cirrus-bulbs are crowded to the margin; testes not in evidence, but folds of the vas deferens still remain on the dorsal side, and, in places occupy the entire thickness of the parenchymatous space. There is a remnant of the ovary with nucleated cells of different sizes and shapes, circular to sub-triangular in outline, embedded in a dense, granular matrix. The principal part of the interior is taken up with the uterus. In sections of my material the contents of the uterus are difficult to interpret. The ova are not sharply defined. The appearance presented is that of masses of thin, membranous structures much collapsed and crumpled, with a few granules, and an occasional nucleated cell. It would appear that the ova are surrounded by thin membranous coverings. Four scoleces and many fragments of strobiles were found; one of the longest measured 160 mm. in length and 2.5 in greatest breadth.

The figures given by Monticelli (1892, figs. 4-6) of the scolex of *Prosthecocotyle forsteri* show diversity similar to what is exhibited by the blackfish cestode. Thus, his figure 4 bears a close resemblance to figure 1 of this paper, in which but one appendage on each bothrium is shown; while in his figure 5 no appendage is visible. The bothria in these cestodes contract strongly so that small structures such as these appendages are, may become so much enveloped by the tissues of the bothria as to be entirely concealed.

In my studies of the two scoleces which I had at first mounted in balsam I noted but one appendage on each bothrium. The transverse sections which had been made of another scolex, unfortunately were inclined to the axis of the scolex, so that, on first examination the presence of more than one appendage on each bothrium was overlooked. Later, the remaining scolex was studied and found to have been fixed in a somewhat expanded condition, so that the presence of three appendages on each bothrium was readily apparent (figs. 2, 3). A restudy of one of the mounted scoleces, in which only one appendage had been noted on the first examination, revealed two posterior appendages showing faintly on two of the bothria. It is possible that a study of living and active scoleces might reveal positions of the posterior appendages which are not shown in the preserved material. Thus, it is conceivable that, in the living and actively functioning bothria, the posterior appendages might be everted so as to appear in a front view

of the bothria. Although the presence of three appendages instead of one on each bothrium would appear to exclude these cestodes of the blackfish from the genus Prosthecocotyle, I have decided to refer them to that genus, in view of the fact that such appendages are easily overlooked, and particularly on account of the very close resemblance which the anatomy of the proglottides bears to that of Monticelli's genus.

It should be noted that the scolex of the genus Moniezoides Fuhrmann (1918:412) bears two appendages which, apparently, have the same structure as those of Prosthecocotyle. The anatomy of the proglottis of that genus, however, is quite different from that of Prosthecocotyle, which renders it unnecessary to discuss the relationship in this place. In neither Moniezoides nor Prosthecocotyle does the anterior bothrial appendage assume the character which gives such aptness to the specific name *Taenia capitellata* Rudolphi, a synonymn of *Tetrabothrius macrocephalus.* For purposes of comparison I have added figures 7 and 8; scolex, and transverse section of scolex, of a cestode which I have referred to the species *Tetrabothrius macrocephalus* (Rudolphi) from the horned grebe (*Colymbus auritus*), Woods Hole, Massachusetts.

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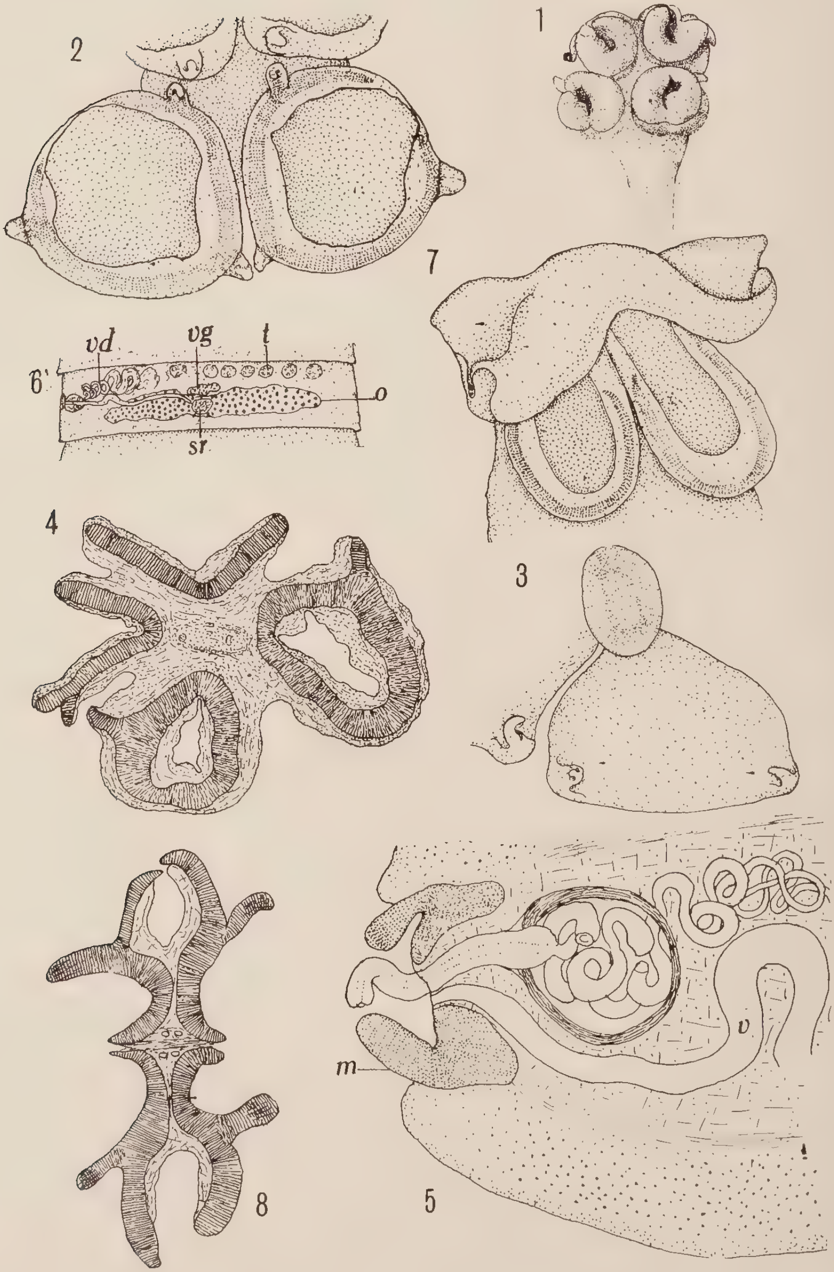

PLATE V

Explanation of Plate V

Prosthecocotyle monticellii sp. nov. from *Globicephalus melas.*

Fig. 1.—Scolex of small specimen in balsam; diameter 0.61 mm. Only one appendage on each bothrium was visible.

Fig. 2.—Portion of scolex in balsam, front view; diameter of bothrium 0.74 mm.

Fig. 3.—View of bothrium from under side; balsam; diameter 0.9 mm.

Fig. 4.—Section of scolex, transverse, but somewhat inclined to axis, passing through an appendage on each of three of the bothria; maximum diameter 1.60 mm.

Fig. 5.—Transverse section of proglottis through cirrus-pouch and genital pore; diameter of cirrus-pouch 0.07 mm. *m,* muscular wall of genital atrium; *v,* vagina.

Fig. 6.—Diagrammatic sketch of adult proglottis; breadth 1.75 mm. *o,* ovary; *sr,* seminal receptacle; *t,* testis; *vd,* vas deferens; *vg,* vitelline gland.

Tetrabothrius macrocephalus (Rudolphi) from *Colymbus auritus.*

Fig. 7.—Scolex, in balsam, dorso-ventral view; length of scolex, 0.56 mm.

Fig. 8.—Transverse section of scolex at about anterior fourth; greatest diameter 0.80 mm.

All figures, except figure 6, from camera lucida sketches.

BOOK REVIEWS

PRÉCIS DE PARASITOLOGIE, Troisième Édition, Entièrement Remaniée. By E. Brumpt, Masson et Cie, Editeurs, Paris, 1922.

The first and second editions of this well known text which appeared in 1910 and 1913 have been deservedly so popular that one welcomes the appearance of this new edition which moreover has been thoroughly revised and is in many respects an entirely new work. It has been so largely increased that despite the elimination of some interesting but not essential features the book has a compass of more than 1,200 pages and as illustrated by 736 figures and 4 colored plates. Nothing demonstrates better the fact that the work is a product of the author than that two-fifths of these figures are originals and one notes with pleasure the absence of time-worn and ancient illustrations which have all too frequently been passed on from author to author for many years. To bring it within reasonable size for handling, the work has been printed on thin paper and while its compass might lead one to question the justification of calling it a compendium its completeness and the ease with which it can be handled must commend it to all workers.

In the scant ten years which have intervened since the appearance of the last edition parasitology has developed rapidly and has undergone fundamental charnges. This condition is of course due rst of all to the war, for with all the conditions that the struggle entailed the transmission of unusual diseases was favored and the difficulty as well as the importance of handling them greatly increased. Then too the number of workers in the field and the vigor of their attack upon its problems were multiplied in even greater ratio. It would be impossible here to do more than outline briefly some of the conspicuous changes in this edition which presents in admirable fashion the additions to knowledge that have resulted from the work of these years.

As might have been expected the additions to the knowledge of the Protozoa are on the whole most extensive. Among the Spirochetes one might note particularly their relations to yellow fever, to dengue and to recurrent fevers. Amoebic dysentery and the causal organism has been intensively studied. The author is at fault in assigning the genus Entamoeba which occurs in man to Leidy. That author gave the name Endamoeba to a cockroach parasite but no evidence has ever been adduced to show that this is the same as the genus which infests man and all general evidence is opposed to that interpretation.

Experimental data are included on the transfer of various species of Leishmania as well as their transmitting agents. The analysis and presentation of the results of the immense amount of work on the pathogenic Trypanosomes is peculiarly successful as well as the discussion of Bartonella and some other newly discovered but not well worked out species.

It is a surprise to see that the author still retains the form Rhinosporidium under the Haplosporidia. The evidence which has been accumulating for sometime that this organism belongs among the plants has reached such volume that one can hardly question the fact and this section should have been transferred to that part of the book dealing with plant parasites.

The section on Trematoda has been enriched by important material on the development of various flukes and by accounts of species that have been discovered or brought into the limelight since the appearance of the earlier edition. One notes with regret the persistence of a few old figures in this section which is perhaps the poorest in the whole work. Unfortunately some of the most recent work on the blood flukes did not reach the author before the manuscript was closed. The development of the broad tapeworm of man is the most important addition noted under the caption Cestoda. However, various minor details have been added at other points in this account.

Much more radical additions have been made to the account of the Nematoda. The most conspicuous item is undoubtedly the discoveries regarding the development of various forms such as the Ascarids. The original view supported strongly by Leuckart and copied into almost every textbook up to date conceived of these forms as following a direct development but recent researches have shown the existence of a complicated life history similar to that demonstrated for the hookworm in the classical studies of Looss. The occurrence of serious eye trouble, and of cutaneous lesions due to Nematodes and the presence in different regions of only recently reported species are among the additions here. While in the main careful to use correct names and justifiable spellings for the zoological species recorded and to follow the rules and decisions of the International Zoological Congress in a fashion to be commended, yet there are occasional slips and one notes with regret the use of Trichocephalus and Ankylostomum.

In the group of Arthropoda especial attention has been given to the important studies on transmitting agents among the blood sucking species. Clinical and experimental data dealing with flea bite and plague, with ticks and recurrent fevers, and with Phlebotomids and cutaneous leishmaniosis are among the items noted.

This work stands almost alone in its consideration of plant parasites which with the exception of the bacteria are presented in much the same manner as the animal parasites. About one-fifth of the book is devoted to this field and the presentation is a good one. It seems clear that in the past this phase of human parasitology has been somewhat neglected and its intensive study will reward the trained investigator although apparently the number of men adequately equipped to undertake research in this field is small.

The style of the author is characteristically French and possesses the brilliant and attractive character of French writings. The book is put together in thoroughy practical form. One must commend especially the careful alphabetic index which has been included. Although hard pressed for room the author has not hesitated to use thirty-two pages for an exhaustive record of the items in the text. All in all the work has been greatly improved in this edition and will easily hold its place of leadership among texts in this field.

NOUVEAU TRAITÉ DE MÉDECINE, Fascicule V, Maladies Infectieuses et Parasitaires (Fin). Masson et Cie, Editeurs, Paris, 1922. 748 pp.

This new volume of the well-known treatise contains so much of interest to parasitologists that its appearance justifies more than passing notice. Some fifteen chapters are occupied each with a single item in the field of parasitic diseases. The especial merit of the treatment lies in the fact that each of these topics is handled by a master in the field and the result is one that in this respect could never be equalled in a volume by a single author although the method has a disadvantage in the lack of coordinated treatment and in slight but evident differences in the plan of individual authors. Among parasitic diseases the following subjects are treated:

Recurrent Fevers by Ch. Nicolle and L. Blaizot; Rat Bite Fever by D. Thibaut; Malaria by H. Vincent and J. Rieux; Kala Azar and Oriental Sore by Ch. Nicolle; Trichinosis by Ch. Joyeux; Filariosis, Strongylosis, Distomatosis, Coccidiosis, and Sarcosporidiosis by J. Guiart; Echinococcosis and Cysticercosis by F. Dévé; Human Trypanosomosis and Bilharziosis by E. Brumpt.

The mention of these names is sufficient to speak for the authoritative and effective presentation of the subject. As appropriate in a treatise on medicine symptomatology, diagnosis, pathology, etiology and similar phases are most thoroughly discussed whereas the morphology of an organism and its zoological relations are considered only briefly or incidentally.

Great care has evidently been devoted to the consideration of the geographic distribution and spread of these parasitic diseases as well as to the means of

prevention which with the clinical factors discussed will be of special service to physicians and students of tropical medicine. They are, indeed, of fundamental importance to all students of parasitology although it must be confessed sometimes slurred over by the laboratory worker. One may fairly ask, however, whether a work of this type would not be more effective in its leadership and less likely to misdirect the field workers in tropical medicine who are naturally inclined to over-emphasize clinical factors, if in connection with its discussions more emphasis had been laid upon the morphology and bionomics of the causative and of the transmitting organisms. One can well understand the necessity of condensation and the impossibility of presenting equally fully all phases of the subject in such a general treatise as that to which this volume belongs, but a brief series of well-selected references to further data on phases of the subject which could not be considered here would in the opinion of the reviewer add greatly to the effectiveness of the work without increasing appreciably its volume. However, this is not a serious defect and parasitologists everywhere will be glad to have so thorough and so successful a presentation of the various topics as is given here.

PALEOPATHOLOGY. By Roy L. Moodie. University of Illinois Press. Urbana, Illinois, 1923.

This work with its 567 pages and 117 plates in addition to numerous other figures is truly a remarkable contribution in a field which save for earlier papers by the same author is practically unworked. Only one of the fifteen chapters is devoted to a consideration of parasitism among fossil animals. Here the author discusses the origin of parasitism, symbiosis among fossil animals, and the few actual cases of parasitism among fossils for which paleontological evidence has been secured. The most prominent of these is the occurrence of galls on carboniferous Crinoids which are due probably to Myzostomids. Moodie cites also the occurrence of mites on ants found in Baltic amber and the probable presence of parasitic Isopods (Bopyridae) in pleistocene Crustacea. To judge this work by the brief record of fossil parasites would do the author a grave injustice. He has gathered together an immense amount of interesting material and has presented the results of his study in clear and attractive fashion. The work has been given a most effective and appropriate presentation by the University of Illinois Press.

NEW HUMAN PARASITES

Taenia infantis Bacigalupo 1922.—A five-year old child who had been passing tapeworm segments was treated with male fern at the Hospital de Ninos, Buenos Aires, Argentina, and expelled a tapeworm 300 mm. long, consisting of 208 segments, with irregularly alternate genital pores, and a head 3 mm. in diameter armed with a double crown of 35 to 40 hooks, the larger of which measured 410 μ, the smaller 260 μ, in length. The gravid segments contained eggs 35 to 40 μ in diameter. Although this worm resembles closely *Taenia crassicollis* of the cat, not heretofore reported as a human parasite, Bacigalup considered it should be looked upon as a distinct species (Semana med., 29: 302-305, Figs. 1-5).